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INTRODUCTION

Few regions in Middle America are so important zoogeographically as is the Isthmus of Tehuantepec, that neck of land connecting North America with Central America, separating the Pacific Ocean from the Gulf of Mexico by a distance of only about 220 kilometers (airline), and forming a low break between the highlands of México and those of Central America. Before World War II the isthmus could be reached readily only by railroad or by ocean vessel to Salina Cruz or Coatzacoalcos. With the advent of roads, principally the Trans-isthmian Highway, vast areas of the interior of the isthmus became accessible to biologists. Nevertheless, long before roads were built in the isthmian region collectors and biologists visited it, especially the town of Tehuantepec, from which collections date back to the 1870's. Therefore, it is rather sur-

prising that no attempt has been made to present a faunal list of the amphibians or reptiles of the isthmus. Ruthven (1912) summarized his collections from the vicinity of Cuatotolapam, Veracruz, and Hartweg and Oliver (1940) presented an annotated list of the species collected by them in the vicinity of Tehuantepec. In recent years there have been only a few papers reporting species from the isthmus (Fugler and Webb, 1957; Langebartel and Smith, 1959). The zoogeographic significance of the Isthmus of Tehuantepec is exemplified by the works of Burt (1931), Duellman (1958), Gloyd (1940), Oliver (1948), and Stuart (1941), who in their discussions of evolution and dispersal of various genera of reptiles, pointed out that the Isthmus of Tehuantepec was a region of zoogeographic importance.

Originally I intended to study the entire herpetofauna of the isthmus. But I have not had opportunity to study all of the reptiles, and I have not had the inclination to solve certain taxonomic problems concerning them. The amphibians that I collected, together with all other known specimens in museums, have been studied. Therefore, the present report is concerned only with the amphibians. Only the amphibians of the lowlands of the isthmus have been sampled adequately. Although I have commented on the highland species in the discussion of distribution, they are not included in the systematic section, which deals solely with the 36 species definitely known to occur in the lowlands of the isthmus.

Among the species of amphibians that I would expect to occur in the isthmus, the only one not yet found there is *Hyla phaeota*. Sufficient specimens of most of the species are available to show their variation in the isthmus. Consequently, the systematics of these amphibians is on a fairly substantial basis. Probably certain species in the isthmian region will be found to be conspecific with others to the south, for example *Hyla ebraccata* with *Hyla leucophyllata* and *Hyla robertmertensi* with *Hyla underwoodi*. Nevertheless, such taxonomic changes will not affect the distributional picture presented here. Our greatest lack of knowledge concerning the amphibians is about their life histories, as may be illustrated by the following questions, all of which now are without definite answers. Where do many of the small frogs conceal themselves during the dry season? What amount of, if any, interspecific competition exists among several species of tree frogs, all of which breed in the same ponds? What factors in the environment permit certain amphibians, but not others, to live in the

humid rainforests, as well as in the arid tropical scrub forest? The answers to these questions and many others must await additional field studies.

The purpose of this paper is to make known the species of amphibians living in the Isthmus of Tehuantepec, to describe the environments in which they live, and to discuss their distribution in the isthmus. With respect to the distribution of animals in the Isthmus of Tehuantepec I will attempt to explain the present patterns of distribution with special reference to climatic fluctuation in the Pleistocene.

Acknowledgments

My extensive field work in the Isthmus of Tehuantepec was made possible by grants from the Penrose Fund of the American Philosophical Society (1956) and the Bache Fund of the National Academy of Sciences (1958). Furthermore, my field work received the hearty support of the Museum of Zoology at the University of Michigan; for their cooperation I am indebted to Norman Hartweg, T. H. Hubbell, and Henry van der Schalie. In the course of my studies I received helpful suggestions from Norman Hartweg, L. C. Stuart, and Charles F. Walker, to whom I am grateful. For permission to examine specimens in their care I thank Doris M. Cochran, Hobart M. Smith, and Richard G. Zweifel. I am deeply indebted to Thomas MacDougall for many suggestions and for aid in preparing the gazetteer. I am most grateful for the efforts of my field companions, Richard E. Etheridge, Jerome B. Tulecke, John Wellman, and especially my wife, Ann S. Duellman, who spent many long days and nights gathering much of the data on which this report is based. Our work in the isthmus was furthered by the generous help and hospitality of many residents, especially the late Wilbur Barker of Tehuantepec, Fortunado Delgado of Rancho Las Hojitas near Acayucan, César Fárjas of Donají, and Juan Mayol of San Andrés Tuxtla. Profesor Jordi Juliá Z. of the Laboratorio de Entomología, Comisión del Papaloapan, Ciudad Alemán, Veracruz, helped make possible my field work in 1959; for this he has my sincere thanks. In conclusion I express my gratitude to Ing. Juan Lozano Franco, Secretaria de Agricultura y Ganadería, for providing me with the necessary permits.

Field Studies in the Isthmus of Tehuantepec

I first visited the Isthmus of Tehuantepec and collected on the Pacific lowlands of the isthmus in July, 1955. At that time heavy rains and impassable roads restricted travelling. In February and March of 1956 my wife and I concentrated our efforts in the central region between the Río Jaltepec and Matías Romero, but also made several trips across the isthmus to gather ecological data in the dry season. In July of the same year, accompanied by Richard E. Etheridge, we again crossed the isthmus several times in order to gather ecological data in the wet season, and studied especially hylid frogs, most of which had not been seen in the dry season. Accompanied by Jerome B. Tulecke and John Wellman, I collected again in the isthmus in July, 1958, between Salina Cruz and Tehuantepec, and between Coatzacoalcos and Coso-

leacaque. In March and April, 1959, I collected at Ciudad Alemán. Nearly 1200 specimens of 30 species of amphibians were thus collected in the Isthmus of Tehuantepec; all specimens are now in the Museum of Zoology at the University of Michigan. Of other species known from the isthmus, I have had field experience with all but one *(Bolitoglossa veracrucis)* in other parts of México.

Sources of Material

There are in museum collections nearly 3000 specimens of amphibians with reliable data from the Isthmus of Tehuantepec. Among the first herpetological specimens collected in the isthmian region are those assembled by Francis Sumichrast in the 1870's from the vicinity of Santa Efigenia and Tapanatepec, Oaxaca. These specimens were sent to the United States National Museum and the Museum National d'Histoire Naturelle in Paris; many served as the types of new species: *Bufo canaliferus* Cope, *Eleutherodactylus rugulosus* Cope, *Syrrhophus leprus* Cope, and *Hylella sumichrasti* Brocchi. In 1911 Alexander G. Ruthven collected in the savanna country near Cuatotolapam, Veracruz; the report on his collections (1912) is the first dealing with the herpetofauna of a part of the isthmus. His specimens are in the collection of the University of Michigan Museum of Zoology. Norman Hartweg and James A. Oliver collected for the University of Michigan Museum of Zoology in the vicinity of Tehuantepec, Oaxaca, during the summer of 1936. The results of their work were published as an annotated list of species occurring on the Pacific slopes of the isthmus (1940). Hobart M. Smith collected in the vicinity of Tehuantepec in January, 1940; his specimens are in the United States National Museum. Specimens collected by Smith served as the types of *Eleutherodactylus avocalis* Taylor and Smith and *Diaglena reticulata* Taylor. Walter W. Dalquest collected vertebrates for the University of Kansas in southern Veracruz in the winters of 1947 and 1948; he spent about six months on the Gulf lowlands of the isthmus, principally in the vicinity of Jesús Carranza. For the past two decades Thomas MacDougall, a resident of New York City, has spent his winters collecting biological specimens in southern México. He makes his headquarters at Tehuantepec, but his compulsion to see the "back country" has taken him to many remote parts of southern Oaxaca. His earlier collections are in the American Museum of Natural History; the later ones are in the University of Illinois Museum of Natural History.

Minor collections include those made by Matthew W. Stirling at San Lorenzo, Veracruz, February-April, 1946 (United States National Museum), by Fred G. Thompson on a trip across the isthmus in December, 1955 (University of Michigan Museum of Zoology), by the University of Kansas Museum of Natural History field party under the direction of Rollin H. Baker at Tolosita, Oaxaca, and by David A. Langebartel and associates from southern Oaxaca in June, 1958 (University of Illinois Museum of Natural History).

In the collections of the United States National Museum are several species of amphibians sent to the museum from Tehuantepec by Francis Sumichrast. These include *Bolitoglossa platydactyla* (USNM 30305, 30344-6, 30528), *Bolitoglossa rufescens* (10042), *Chiropterotriton chiropterus* (30347), *Lineatriton lineola* (30353), *Parvimolge townsendi* (30352), *Pseudoeurycea cephalica* (30350), *Thorius pennatulus* (30348-9), *Hyla miotympanum* (30302-3),

and *Hyla picta* (30304). Because of the poor condition of the specimens, determinations of those listed as *Bolitoglossa rufescens* and *Pseudoeurycea cephalica* are uncertain. With the exception of the *Bolitoglossa rufescens*, which is stated to have come from Santa Efigenia, all of these specimens are catalogued as having come from Tehuantepec. None of these species has since been recorded from the Pacific slopes of the isthmus; however, they all occur in the vicinity of Orizaba, Veracruz. Probably Sumichrast carried the specimens with him from Orizaba, his home before moving to Santa Efigenia, and shipped them from Tehuantepec to the United States National Museum. These species definitely should not be considered as inhabitants of the Pacific slopes of the Isthmus of Tehuantepec.

DESCRIPTION OF THE ISTHMUS OF TEHUANTEPEC

The Isthmus of Tehuantepec is a strip of land forming a low pass, which separates the mountain masses of México proper from those of Central America, and at the same time provides a continuum of lowlands from the Gulf of Mexico to the Pacific Ocean. This topography combines with the climatic conditions to create extremely diverse environments, the distribution of which can be adequately understood only after an acquaintance with the topography and climate of the region.

Physiography

In east-central Oaxaca the mountain masses comprising the Sierra Madre Oriental and the Sierra del Sur terminate in a series of ranges—Sierra de Juárez, Sierra de los Míjes, and Sierra de Choapam. From lofty peaks, such as Cerro de Zempoaltepetl (3400 meters), the highlands diminish eastward to succeedingly lower ridges, until in the middle of the Isthmus of Tehuantepec the continental divide is about 250 meters above sea level. Eastward from this low divide the land rises to form the Sierra Madre de Chiapas, which is continuous with the highland masses of Guatemala.

For the purposes of this description, the lowlands of the isthmus may be divided into three parts—the Gulf Coastal Plain, the central ridges, and the Pacific Coastal Plain, which in the isthmus is called the Plains of Tehuantepec (Figs. 1 and 2).

The Gulf Coastal Plain is broad and fairly level near the coast, but rolling in the interior. The plain, throughout most of its length in the isthmus, is at least 75 kilometers wide. The majority of the region in the isthmus is drained by the Río Coatzacoalcos, which flows in a northerly course to the Gulf of Mexico. The western part is drained by the Río San Juan, the principal tributary of the Río Papaloapan. Behind the coastal dunes are frequent, and some-

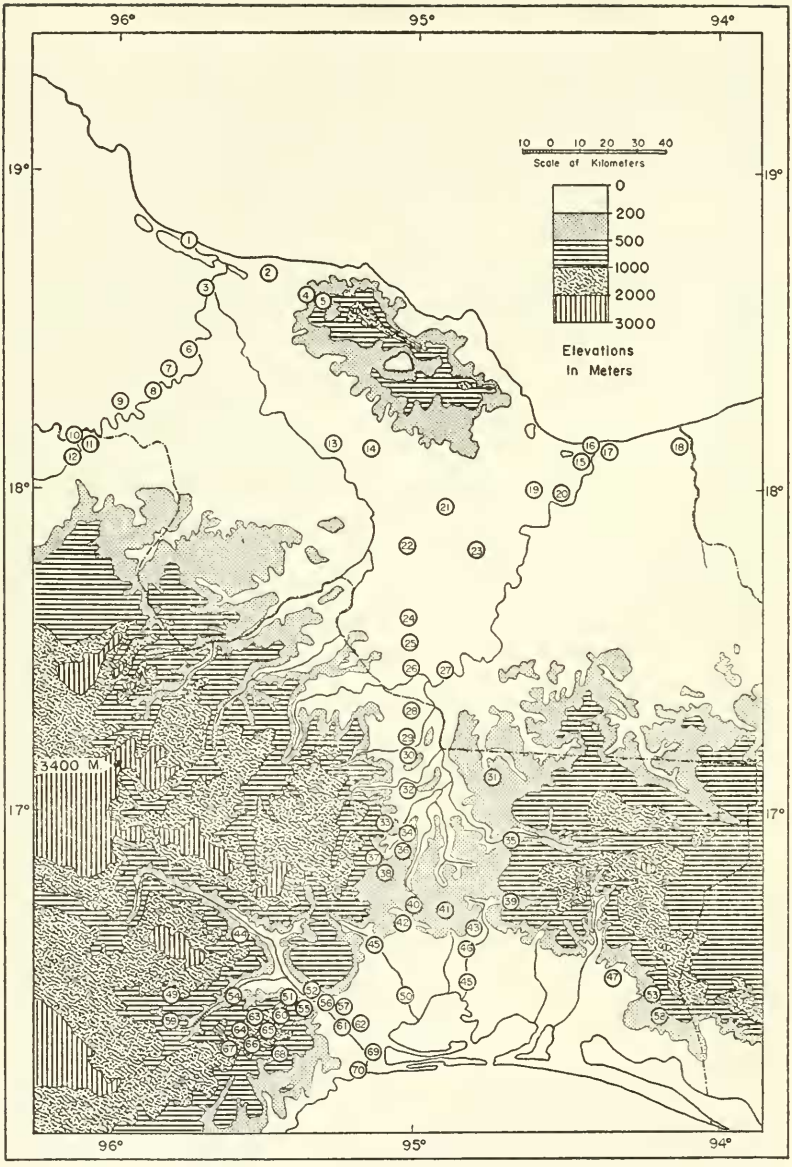

FIG. 1. Map of the Isthmus of Tehuantepec based on the American Geographical Society's "Map of Hispanic America on the Scale of 1:1,000,000."

The localities shown are numbered in the gazetteer; the numerical sequence of localities is an arrangement whereby north takes precedence over south and west over east. 1. Alvarado. 2. Lerdo de Tejada. 3. Tlacotalpan. 4. Tula. 5. Tecolapan. 6. Amatitlán. 7. Cosamaloapan. 8. Chacaltianguis. 9. Novillero. 10. Ciudad Alemán. 11. Papaloapan. 12. Tuxtepec. 13. Cuatotolapam. 14. Hueyapan. 15. Berta. 16. Coatzacoalcos. 17. Ayentes. 18. Río de las Playas. 19. Cosaleacaque. 20. Minatitlán. 21. Acayucan. 22. Aquilera. 23. San Lorenzo. 24. Naranja. 25. Suchil. 26. Jesús Carranza. 27. La Oaxaqueña. 28. Ubero. 29. Donají. 30. Tolosita. 31. El Modelo. 32. Sarabia. 33. Guichicovi. 34. La Princesa. 35. Santa María Chimalapa. 36. Matías Romero. 37. Santo Domingo Petapa. 38. El Barrio. 39. Palmar. 40. Chivela. 41. Santiago Chivela. 42. Nizanda. 43. Agua Caliente. 44. Portillo Los Nanches. 45. Ixtepec. 46. La Ventosa. 47. Zanatepec. 48. Unión Hidalgo. 49. Tres Cruces. 50. Juchitán. 51. Escurano. 52. Salazar. 53. Santa Efigenia. 54. Tequisistlán. 55. Cerro de Quiengola. 56. San Pablo. 57. Mixtequilla. 58. Tapanatepec. 59. Zarzamora. 60. Limón. 61. Tehuantepec. 62. Bisilana. 63. Santa Lucía. 64. Cerro de Arenal. 65. Cerro de San Pedro. 66. La Concepción. 67. Tenango. 68. San Antonio. 69. Huilotepec. 70. Salina Cruz.

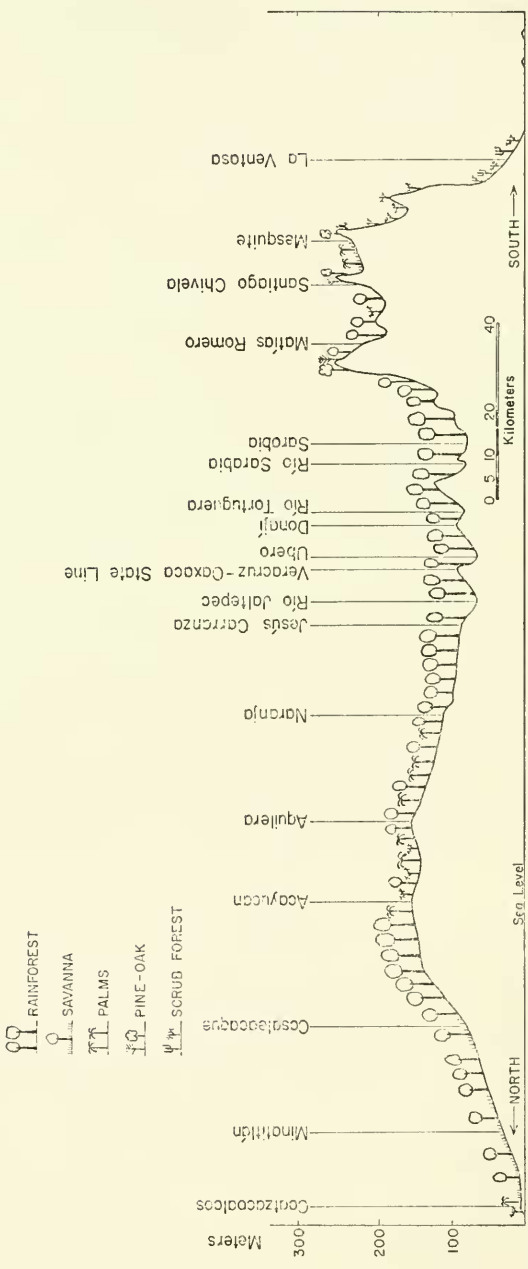

FIG. 2. Topographic profile of the Isthmus of Tehuantepec showing major localities along the Trans-isthmian Highway and major types of vegetation. Vertical exaggeration approximately 165 times.

times large, lagoons. Immediately inland from Coatzacoalcos and along the lower stretches of the Río Papaloapan are extensive marshes. Essentially the entire coastal plain, with the exception of the coastal dunes, consists of rich alluvial deposits.

The central ridges extend from the Río Jaltepec southward to within 40 kilometers of the Pacific coast. It is in this area that the continuity of the high ridges and volcanic peaks, which extend nearly the entire length of the Americas, is interrupted at a point almost directly in line with the shortest distance between the two oceans. The northern part of this central region consists of hills dissected by tributaries of the Río Coatzacoalcos; the principal ones from north to south are—Río Jaltepec, Río Tortuguero, Río Sarabia, and Río Malatengo. The plains of Chivela are south of these rivers and lie at an elevation of about 200 meters; at the southern edge of these plains a range of hills rises to 250 to 400 meters above sea level. These hills drop abruptly to the Plains of Tehuantepec. In the northern and central parts of this central region the rocks are granitic; the hills to the south of the Plains of Chivela are limestone.

The Pacific Coastal Plain or Plains of Tehuantepec have a maximum width of about 30 kilometers. From the base of the hills at an elevation of about 75 meters the plains slope gradually to the sea. To the west of the Río Tehuantepec and to the east of the Plains of Tehuantepec at the base of the Sierra Madre de Chiapas, the coastal plain becomes much narrower; in these places the continuity of the plain is frequently interrupted by low north-south ridges extending outward from the mountains or by isolated hills. The soil is poor, varying from volcanic rock to gravel and sand.

Climate

The prevailing winds are from the north across the Gulf of Mexico. These moisture-laden winds precipitate most of their moisture north of the central ridges. This results in high rainfall on the northern slopes and Gulf Coastal Plain and relatively little rainfall on the southern slopes and the Pacific Coastal Plain. Precipitation is cyclic; there is a marked wet and a dry season throughout the region, but this is most noticeable on the Pacific lowlands (Fig. 3). At Salina Cruz on the Pacific Ocean the average annual rainfall is 1040 mm. (Contreras, 1942); of this amount, only 15 mm. falls from November through April. On the Gulf Coastal Plain (Minatitlán station) the average annual

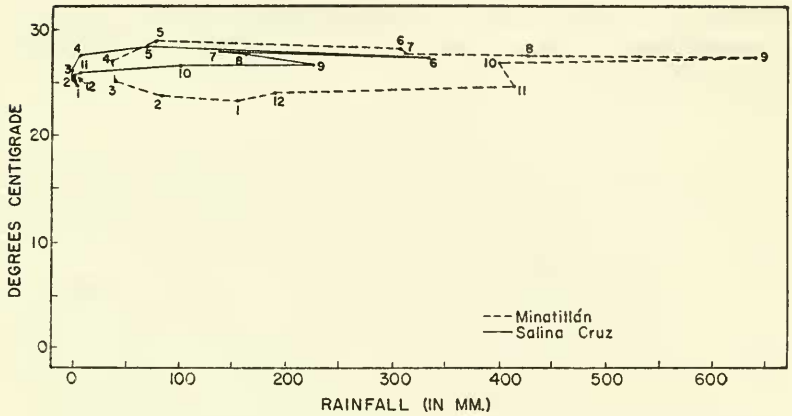

FIG. 3. Climatographs for Minatitlán, Veracruz, and Salina Cruz, Oaxaca, based on data given by Contreras (1942). Plotted points are for mean monthly temperatures and rainfall; months are indicated by numbers.

rainfall is 3085 mm. In this region the driest months are February through May, during which time 236 mm. of rain falls. At Salina Cruz the wettest month is June; at Minatitlán it is September. There is little variation in temperature throughout the isthmus; the average annual temperature at Salina Cruz is 26.6° C.; that at Minatitlán is 26.2° C. During the winter when masses of air from the arctic move southward into the Great Plains of the United States, cool winds blow across the isthmus. These are usually accompanied by overcast sky and sometimes a slight amount of precipitation. These "nortes" may cause a drop in temperature of about six to eight degrees in a few hours.

Vegetation

The topography and climate combine to produce drastically different types of climax vegetation on the northern and southern lowlands of the isthmus. The picture is somewhat complicated by the savannas on the Gulf Coastal Plain, which, as will be shown later, are dependent upon edaphic features more than climatic conditions. The following brief account of the vegetation in the Isthmus of Tehuantepec is based on data provided by Williams (1939) and Goldman (1951), supplemented by personal observations. The purpose of this description is not to analyze the flora of the isthmus, but to give the reader a picture of this aspect of the biota of the major environments with which I shall be concerned in the ensuing discourse on the amphibians of the region.

The three divisions of the isthmus recognized in the account of the physiography serve equally well in describing the vegetation. Those divisions are as follows:

Gulf Lowlands

On the lowlands north of the continental divide and extending to the Gulf of Mexico are three major types of vegetation—tropical rainforest, arid tropical scrub forest, and savanna. Aside from these, there are marshes and lagoons near the coast.

On the coastal dunes there are thickets of sea grape, patches of *Cenchrus,* and clumps or scattered *Opuntia.* The lagoons are bordered by mangrove thickets made up primarily of *Lonchocarpus hondurensis.* In the marshes along the lower Río Coatzacoalcos and Río Papaloapan the tall tough grass, *Gynerium sagittatum,* is common.

According to Beard (1953: 291) the development of savanna vegetation is dependent upon soil, topography, and drainage. Level regions having permeable soil horizons lying on top of an impermeable horizon provide poor drainage. In most savanna regions in the Americas the grasslands become waterlogged or even partly flooded during the rainy season and desiccated in the dry season. Many ecologists and phytogeographers have postulated that savannas are either man made or are examples of a fire climax. Beard (*op. cit.:* 203) provided multitudinous evidence that the association of savanna vegetation and certain types of edaphic and topographic conditions was so strongly marked that grassland is the natural vegetation in these areas.

Savannas are scattered through southern Veracruz eastward to British Honduras. These usually are grasslands having scattered trees or clumps of trees around depressions, which may contain water throughout the year (Pl. 1, fig. 1). According to Williams (*op. cit.*), the most common trees in the savannas in southern Veracruz are *Ceiba pentandra, Chlorophora tinctoria,* and *Brysonima crassifolia.*

Lying in a rain shadow cast by the Tuxtlas and on sandy and well-drained soils is a dense xerophytic forest. The crown of this deciduous forest usually is little more than ten to twelve meters above the ground (Pl. 1, fig. 2). Conspicuous trees in this scrub forest are *Acacia cornigera, Bauhinia latifolia, Calliandra bijuga, Cassia laevigata, Guazuma ulmifolia,* and various species of *Bursera.*

The most extensive type of vegetation on the Gulf Coastal Plain is a tall evergreen forest resembling tropical rainforest. Although

this forest is made up of many species of trees that are characteristic of true rainforest, the forest on the Gulf Coastal Plain cannot be classified as true rainforest, neither by the climatic conditions, nor the structure of the forest. The seasonal variation in rainfall probably is the chief factor in hindering the development of a rainforest climax vegetation. Usually a minimum of 65 mm. of rainfall each month is considered essential for the development of true rainforest. At Minatitlán the average rainfall for March (39 mm.) and April (36 mm.) is far below this minimum. Structurally, this forest has a crown about 30-35 meters above the ground but individual trees rising five meters or more above the crown (Pl. 2, figs. 1-2). There is no clear stratification within the forest; in many parts of it there are dense growths of bushes, small trees, and palms. The forest on the Gulf Coastal Plain, therefore, most properly might be referred to as a quasi-rainforest, a term that has been applied to other such forests in tropical America.

Among the abundant and dominant trees in this forest are *Swietenia macrophylla, Calophyllum brasiliense, Achras zapota, Ceiba pentandra, Castilla elastica, Cedrela mexicana, Tabebuia Donnell-Smithi, Calocarpum mammosum, Bombax ellipticum,* and a variety of *Ficus.* Epiphytes and lianas are abundant.

Central Ridges

The vegetation of the central ridges of the isthmus is, for the most part, transitional between the tall rainforest of the Gulf Coastal Plain and the low xerophytic scrub forest of the semi-arid Pacific Coastal Plain. On the northern slopes of the ridges the rainforest is more poorly developed than on the plains to the north. Many of the same species of trees are present, including *Ceiba pentandra, Cedrela mexicana, Swietenia macrophylla,* and *Ficus* sp.; nevertheless, these seldom are as large as members of the same species in the forest on the plains. Other species present on the forested slopes include *Tabebuia Donnell-Smithi, Zanthoxylum melanostictum, Pithecolobium arboreum,* and a species of *Pterocarpus.* The structure of this forest differs from that on the Gulf Coastal Plain in that there is no continuous upper canopy and there is a dense undergrowth (Pl. 3, fig. 1). This type of forest extends from Mogoñe southward to about Matías Romero.

In the vicinity of Matías Romero open pine-oak forest (*Pinus caribaea* and *Quercus* sp.) is found on some ridges as low as 250 meters above sea level.

On the Plains of Chivela in the southern part of the central region

the vegetation takes on a semi-arid appearance, especially in a savanna on the plains. Clumps of small trees and bushes, consisting of *Croton nivea, Cordia cana, Jacquinia aurantiaca, Calycophyllum candidissimum,* and *Cassia emarginata,* are scattered on a grassy plain, from which rise widely-spaced palms of an unknown species (Pl. 3, fig. 2).

Pacific Coastal Plain

The vegetation of the Pacific lowlands definitely is semi-arid in character. Most of the trees are deciduous, thorny, and short. During the dry season the landscape presents a barren appearance, but shortly after the first summer rains dense green foliage appears (Pl. 4, figs. 1 and 2). Between Juchitán and La Ventosa few trees are more than two meters high (Pl. 5, fig. 1). In many areas the trees and bushes form an almost impenetrable tangle, whereas on especially rocky soils or on slopes those plants are more widely spaced. Abundant and widespread species of trees on the Plains of Tehuantepec include *Acacia cymbispina, Prosopis chilensis, Caesalpinia coriaria, Caesalpinia eriostachys, Celtis iguanaea, Cordia brevispicata, Jatropha aconitifolia,* and *Crescentia alata.*

Montane Vegetation

In order to illustrate the interruption of subtropical and temperate types of vegetation by the lowlands of the Isthmus of Tehuantepec, it is necessary to digress for a moment from the isthmus and consider the types of vegetation present on the adjacent highlands. On the higher peaks, such as Cerro de Zempoaltepetl, above about 2500 meters is fir forest (*Abies religiosa*); lower on the slopes are extensive pine forests, which on some slopes are mixed with oak or replaced entirely by oaks. Subtropical cloud forest, characterized by relatively cool temperatures and high humidity, is found at elevations usually between 1000 and 1800 meters on the windward slopes of the Sierra Madre Oriental in Veracruz and northern Oaxaca and on the northern and southern slopes of the Chiapan-Guatemalan Highlands. None of these forest types is continuous across the Isthmus of Tehuantepec.

The Sierra de los Tuxtlas

Although actually located in the region of the Isthmus of Tehuantepec, the Sierra de los Tuxtlas, because of its isolated position, need not be considered in great detail in analyzing the distribution of animals inhabiting the lowlands of the isthmus. Nevertheless

because some species living in the highlands adjacent to the isthmus also live in the Tuxtlas, this range is briefly described here. The Sierra de los Tuxtlas is a range of volcanos lying near the Gulf Coast in southern Veracruz between the mouths of the Río Papaloapan and the Río Coatzacoalcos. Volcán San Martín, the highest peak, rises above 1800 meters. This range of volcanos is surrounded by lowlands, which immediately to the south and west are covered with savanna and in places by scrub forest. The luxuriant nature of the vegetation on these volcanos indicates that this range receives much more rainfall than the surrounding lowlands. Especially on the northern slopes, tropical rainforest is well developed; this is replaced at about 1200 meters by cloud forest. The southern and western slopes are drier, for the lower slopes are covered with a scrubby, but evergreen, forest.

Detailed comments on the herpetofauna of the Tuxtlas have been omitted purposefully, for the reptiles and amphibians of the region currently are being studied by Douglas Robinson.

GAZETTEER

The following localities are those referred to in the text. The name of the locality (listed alphabetically by states) is followed by latitude, longitude, elevation, general description (town, ranch, etc.), and general type of habitat. Unless otherwise noted, distances are straight-line (airline) distances in kilometers. The localities have been plotted from the American Geographical Society's "Map of Hispanic America on the Scale of 1:1,000,000" (Millionth Map). Numbers in brackets identify the position of a locality on the accompanying map (Fig. 1).

Oaxaca

Agua Caliente.—Lat. 16° 38′; long. 94° 48′; elev. 140 m. A hot spring, 6.9 km. north of La Ventosa on the Trans-Isthmian Highway; arid scrub forest [43].

Arenal, Cerro de.—Lat. 16° 18′; long. 95° 32′; elev. 925 m. (crest). A ridge northeast of Tenango; scrub forest on slopes and pine-oak forest on top [64].

Barrio, El.—Lat. 16° 38′; long. 95° 07′; elev. 314 m. A village about 10 kilometers southwest of Matías Romero; transition between scrub forest and broadleaf hardwood forest [38].

Bisilana.—Lat. 16° 20′; long. 95° 13′; elev. 35 m. A place name for a former ranch at the edge of Tehuantepec; open arid scrub forest [62].

Chivela.—Lat. 16° 20′; long. 95° 01′; elev. 195 m. A village on the Trans-isthmian Railroad, 26 kilometers by rail south of Matías Romero and on the western edge of the semi-arid Plains of Chivela [40].

Concepción.—Lat. 16° 17′; long. 95° 29′; elev. 1200 m. A ranch on the slopes of Cerro Arenal, east-northeast of Tenango; dry pine-oak forest [66].

Coyol.—Exact position unknown; according to Smith and Taylor (1950: 10), Coyol is "between San Antonio and Las Cruces."

Donají.—Lat. 17° 13′; long. 95° 02′; elev. 90 m. A village at Km. 155 on the Trans-isthmian Highway; rainforest [29].

Escurano.—Lat. 16° 25′; long. 95° 27′; elev. 500 m. A ranch about 25 kilometers west-northwest of Tehuantepec; arid scrub forest [51].

Guichicovi, San Juan.—Lat. 16° 58′; long. 95° 06′; elev. 250 m. A village on the north slopes of the isthmus, 12 kilometers north-northwest of Matías Romero; cleared hardwood forest and coffee plantations [33].

Huilotepec.—Lat. 16° 14′; long. 95° 09′; elev. 30 m. A small village on the Río Tehuantepec, 13 kilometers south-southeast of Tehuantepec; open arid scrub forest [69].

Ixtepec.—Lat. 16° 34′; long. 95° 06′; elev. 60 m. A town and railroad junction on the northwestern edge of the Plains of Tehuantepec; arid scrub forest [45].

Juchitán.—Lat. 16° 26′; long. 95° 02′; elev. 15 m. A town on the Plains of Tehuantepec, 22 kilometers by road east-northeast of Tehuantepec; arid scrub forest [50].

Limón.—Lat. 16° 20′; long. 95′ 29°; elev. 600 m. A former agrarian colony and now a small ranch about 27 kilometers west of Tehuantepec; arid scrub forest [60].

Matías Romero.—Lat. 16° 53′; long. 95° 02′; elev. 200 m. A town on the Trans-isthmian Highway and railroad in the hills near the crest of the isthmus; broadleaf hardwood forest and open pine-oak forest [36].

Mixtequilla.—Lat. 16° 24′; long. 95° 18′; elev. 40 m. A village on the Río Tehuantepec, northwest of Tehuantepec; dense scrub forest [57].

Modelo, El.—Lat. 17° 07′; long. 94° 43′; elev. 200 m. An old rubber plantation on the Río Chalchijapa, a tributary to the Río Coatzacoalcos; rainforest [31].

Nanches, Portillo Los.—Lat. 16° 35′; long. 95° 37′; elev. 500 m. A place name, about 4 kilometers southeast of Totolapilla; scrub forest [44].

Nizanda.—Lat. 16° 42′; long. 95° 02′; elev. 150 m. A village on the Trans-isthmian Railroad between Chivela and Ixtepec; dense scrub forest [42].

Nueva Raza.—Exact location unknown; according to Thomas MacDougall, this locality is in the lowlands of northern Oaxaca; rainforest.

Palmar.—Lat. 16° 43′; long. 94° 40′; elev. 300 m. A small ranch on the west base of Cerro Atravesado; scrub forest [39].

Papaloapan.—Lat. 18° 11′; long. 96° 06′; elev. 25 m. A small village on the Río Papaloapan in northern Oaxaca; low evergreen forest and savanna [11].

Princesa, La.—Lat. 16° 56′; long. 95° 02′; elev. 150 m. A ranch on the northern slopes of the isthmus, 6 kilometers by road north of Matías Romero; poorly developed rainforest [34].

Quiengola, Cerro de.—Lat. 16° 24′; long. 95° 22′; elev. 900 m. (crest). A hill 15 kilometers west-northwest of Tehuantepec; dense scrub forest on slopes and scattered pines on top [55].

Salazar.—Lat. 16° 25′; long. 95° 20′; elev. 45 m. A ranch on the Río Tehuantepec, northwest of Tehuantepec; dense scrub forest [52].

Salina Cruz.—Lat. 16° 10′; long. 95° 12′; sea level. A port on the Golfo de Tehuantepec; open arid scrub forest [70]. Collections were made in the vicinity of the town and in the open scrub forest 2.4 kilometers north at an elevation of 20 meters.

San Antonio.—Lat. 16° 15′; long. 95° 22′; elev. 40 m. A ranch about 25 kilometers west-southwest of Tehuantepec; arid scrub forest [68].

San Pablo.—Lat. 16° 24′; long. 95° 18′; elev. 40 m. A ranch on the Río Tehuantepec, northwest of Tehuantepec; dense scrub forest [56]. Cerro San Pablo probably is the hill north of this ranch; this is shown on some maps as Cerro de los Amates.

San Pedro, Cerro de.—Lat. 16° 18′; long. 95° 28′; elev. about 1100 m. (crest). A ridge about 24 kilometers west of Tehuantepec and east of Cerro Arenal; scrub forest on slopes and pine-oak forest on top [65].

Santa Efigenia.—Lat. 16° 25′; long. 94° 13′; elev. 500 m. A ranch on the southern slopes of the Sierra Madre de Chiapas, 8 kilometers north-northwest of Tapanatepec; scrub forest. Former home of Francis Sumichrast [53].

Santa Lucía.—Lat. 16° 18′; long. 95° 28′; elev. 800 m. A place name for a former ranch on the east slopes of Cerro Arenal; scrub forest [63].

Santa María Chimalapa.—Lat. 16° 55′; long. 94° 42′; elev. 296 m. A village on the Río de los Milagros, a tributary to the Río Coatzacoalcos; rainforest [35].

Santiago Chivela.—Lat. 16° 42′; long. 94° 53′; elev. 200 m. A village on the Trans-isthmian Highway, 13.4 kilometers by road south of Matías Romera; dry, grassy plains and scattered clumps of scrubby trees and palms [41]. Collections were made in the vicinity of the village and at a rocky stream, 11 kilometers south on the Trans-isthmian Highway at an elevation of 230 m.

Santo Domingo (Petapa).—Lat. 16° 50′; long. 95° 08′; elev. 225 m. A village about 13 kilometers west-southwest of Matías Romero; semi-arid scrub forest [37].

Sarabia.—Lat. 17° 04′; long. 95° 02′; elev. 100 m. A village 25 kilometers north of Matías Romero on the Trans-isthmian Highway; rainforest [32]. Collections were made in the vicinity of the village and in the rainforest along the Río Sarabia, 5 kilometers north of the village at an elevation of 80 meters.

Tapanatepec.—Lat. 16° 32′; long. 94° 12′; elev. 90 m. A town on the Pan-American Highway on the lower slopes of the Sierra Madre de Chiapas; dense scrub forest [58].

Tehuantepec.—Lat 16° 20′; long. 95° 14′; elev. 35 m. A large town on the Plains of Tehuantepec; scrub forest [61]. Collections were made in the vicinity of the town and in the dense scrub forest 8.6 kilometers west at an elevation of 85 meters and 14 kilometers west at an elevation of 120 meters.

Tenango.—Lat. 16° 16′; long. 95° 30′; elev. 1100 m. A town in the mountains about 40 kilometers west-southwest of Tehuantepec; scrub forest [67].

Tequisistlán.—Lat. 16° 24′; long. 95° 37′; elev. 190 m. A village in the valley of the Río Tequisistlán, a tributary to the Río Tehuantepec; dense scrub forest [54]. Most collections were made about one kilometer north of the village where the Pan-American Highway crosses the Río Tequisistlán.

Tolosita.—Lat. 17° 12′; long. 95° 03′; elev. 80 m. A village on the Río Tortuguero near the Trans-isthmian Highway; rainforest [30].

Tres Cruces.—Lat. 16° 26′; long. 95° 51′; elev. 750 m. A ranch near the Pan-American Highway, 70 kilometers by road west-northwest of Tehuantepec; dense scrub forest [49].

Tuxtepec.—Lat. 18° 06′; long. 96° 05′; elev. 80 m. A town on the Río Papaloapan in northern Oaxaca; low evergreen forest [12].

Ubero.—Lat. 17° 18′; long. 95° 00′; elev. 80 m. A lumber camp and railroad station, 8.5 kilometers south of the Río Jaltepec on the Trans-isthmian Highway; rainforest [28].

Unión Hidalgo.—Lat. 16° 27′; long. 94° 48′; elev. 7 m. A village on the railroad, 20 kilometers east-northeast of Juchitán; open scrub forest [48].

Ventosa, La.—Lat. 16° 30′; long. 94° 51′; elev. 25 m. A village at the junction of the Pan-American and Trans-isthmian highways; open scrub forest [46].

Zanatepec.—Lat. 16° 28′; long. 94° 22′; elev. 80 m. A village on the Pan-American Highway at the eastern edge of the Plains of Tehuantepec; dense scrub forest [47]. Most collections were made in the scrub forest 5 to 8 kilometers west-northwest of the village.

Zarzamora.—Lat. 16° 21′; long. 95° 48′; elev. 800 m. A ranch between La Reforma (16 kilometers west of Tequisistlán) and Santa María Ecatepec; scrub forest with oaks on higher ridges [59].

Veracruz

Acayucan.—Lat. 17° 57′; long. 94° 55′; elev. 160 m. A large town on the Trans-isthmian Highway; rainforest [21]. Collections were made in the vicinity of the town, but principally at Rancho Las Hojitas, 7 kilometers northwest of town at an elevation of 150 meters.

Alvarado.—Lat. 18° 47′; long. 95° 47′; sea level. A fishing village at the mouth of the Río Papaloapan; coastal dunes and marshes [1]. Most collections were made 1-3 kilometers southeast of the village in marshes on the leeward side of the coastal dunes.

Amatitlán.—Lat. 18° 26′; long. 95° 45′; elev. 4 m. A village on the bank of the Río Papaloapan; savanna and sugar plantations [6].

Aquilera.—Lat. 17° 48′; long. 95° 01′; elev. 150 m. A village 21 kilometers southwest of Acayucan on the Trans-isthmian Highway; rainforest [22].

Ayentes.—Lat. 18° 10′; long. 94° 26′; elev. 2 m. A railroad station on the east bank of the Río Coatzacoalcos, across the river from the city of Coatzacoalcos; scrub forest and marshes [17].

Berta.—Lat. 18° 07′; long. 94° 27′; elev. 5 m. A ranch just south of Coatzacoalcos; scrub and low evergreen forest [15].

Chacaltianguis.—Lat. 18° 18′; long. 95° 52′; elev. 5 m. A village on the Río Papaloapan; savanna [8].

Ciudad Alemán.—Lat. 18° 13′; long. 96° 07′; elev. 30 m. A new government town, headquarters of the Comisión del Papaloapan; scrub and low evergreen forest [10].

Coatzacoalcos (formerly Puerto México).—Lat. 18° 10′; long. 94° 27′; elev. 2 m. A seaport at the mouth of the Río Coatzacoalcos; scrub on coastal dunes; marshes and low evergreen forest inland [16]. Most collections are from the forest-savanna ecotone, 8 kilometers southwest of town.

Cosamaloapan.—Lat. 18° 22′; long. 95° 50′; elev. 4 m. An agricultural town on the Río Papaloapan; savanna and sugar plantations [7].

Cosoleacaque.—Lat. 17° 59′; long. 94° 38′; elev. 55 m. A village 8 kilometers by road west of Minatitlán; savanna [19].

Cuatotolapam.—Lat. 18° 08′; long. 95° 16′; elev. 13 m. A village on the Trans-isthmian Railroad; savanna and low evergreen forest along streams [13].

Hueyapan.—Lat. 18° 08′; long. 19° 09′; elev. 85 m. A town 32 kilometers by road northwest of Acayucan; savanna and low evergreen forest [14]. Collections were made in the vicinity of the town and from forest 10 kilometers southeast of town at an elevation of 135 meters.

Jesús Carranza (formerly Santa Lucrecia).—Lat. 17° 27′; long. 95° 02′; elev. 80 m. A town and railroad junction in the middle of the isthmus; rainforest [26]. Most of Dalquest's specimens came from varying distances from Jesús Carranza along the Río Coatzacoalcos and its tributaries.

Minatitlán.—Lat. 17° 58′; long. 94° 32′; elev. 15 m. An oil refinery center on the Río Coatzacoalcos; savanna [20].

Naranjo.—Lat. 17° 35′; long. 95° 07′; elev. 100 m. A village on the Trans-isthmian Highway, 45 kilometers south of Acayucan; rainforest and palm forest [24].

Novillero.—Lat. 18° 16′; long. 95° 59′; elev. 10 m. A village on the Río Papaloapan; scrub forest and grassland [9].

Oaxaqueña, La.—Lat. 17° 26′; long. 94° 53′; elev. 80 m. A hacienda on the Río Coatzacoalcos about 12 kilometers east of Jesús Carranza; rainforest [27].

Playas, Río de las.—Lat. 18° 08′; long. 94° 07′; elev. 3 m. The river (sometimes known as the Río Tonolá) forming the boundary between the states of Veracruz and Tabasco; rainforest [18].

San Lorenzo.—Lat. 17° 44′; long. 94° 42′; elev. 25 m. A village on the Río Chiquito, about 30 kilometers southeast of Acayucan; rainforest [23].

Suchil.—Lat. 17° 31′; long. 95° 03′; elev. 40 m. A village on the Trans-isthmian Railroad, about 10 kilometers north of Jesús Carranza; rainforest [25].

Tecolapan.—Lat. 18° 24′; long. 95° 18′; elev. 275 m. A village on a small river of the same name in the western foothills of Los Tuxtlas; rainforest [5].

Tejada, Lerdo de.—Lat. 18° 37′; long. 95° 31′; elev. 60 m. An agricultural village, 35 kilometers by road east-southeast of Alvarado; scrub forest, marshes, and sugar plantations [2]. Collections were made in a marsh, 5 kilometers west-northwest of the village.

Tlacotalpan.—Lat. 18° 37′; long. 95° 42′; elev. 3 m. A town at the confluence of the Río San Juan and Río Papaloapan; marshes and sugar plantations [3].

Tula.—Lat. 18° 36′; long. 95° 22′; elev. 150 m. A village near the western base of Los Tuxtlas; low evergreen forest and marshes [4]. Collections were made in a marsh 3 kilometers northwest of the village.

THE AMPHIBIAN FAUNA OF THE LOWLANDS

In presenting an account of the amphibian fauna of the lowlands of the Isthmus of Tehuantepec three items must be considered:

1. The composition of the fauna.
2. The ecology of the fauna.
3. The distribution of the fauna.

These items, together with similar data concerning the amphibians of the adjacent highlands, will form the basis for the subsequent discussion of the establishment of present patterns of distribution in the isthmian region.

Composition of the Fauna

The amphibian fauna of the lowlands of the Isthmus of Tehuantepec consists of 36 species definitely recorded from the area. These include one genus and species of caecilian, one genus, including three species of salamanders, and 14 genera and 32 species of anurans.

In comparison with the known amphibian fauna of the forested and savanna portions of El Petén, Guatemala (Stuart, 1935 and 1958), we find that there are more species recorded from the isthmus than from El Petén. Stuart found only 20 species of amphibians in both forest and savanna habitats in El Petén. Of the 36 species of amphibians known from the isthmus, 28 occur on the Gulf lowlands and live in forest or savanna habitats.

The geographic position of the isthmus with regard to major faunal areas in Middle America, and the diversity of the environment are important factors in understanding the presence of a large number of species of amphibians in the isthmus. The large number of species probably is a reflection of the diversity of the environment; this diversity is the result of fluctuation of climate, and thus

environments, in the not too distant past. In no individual habitat, such as rainforest, savanna, or scrub forest, does the number of species approach the total for the region.

Ecology of the Fauna

In the preceding section on the description of the Isthmus of Tehuantepec I have outlined the major environments in the region. With respect to the distribution of amphibians we may recognize three major environments in the isthmus—rainforest, semi-arid scrub forest, and savanna. Each of these has varying combinations of physical and biotic factors that are important in the ecology of amphibians. Because of the importance of moisture, not only for the maintenance of life in these animals, but in most species their dependence on water for breeding purposes, this environmental factor is considered the most significant in the ecological distribution of amphibians. A second factor is the availability of necessary shelter, especially aestivation sites. These factors will be compared in the three major environments in the region.

Moisture is present in the environment in the form of free water or atmospheric moisture. With respect to the latter, it is well known that dense shaded forests have a considerably higher relative humidity than do open plains or areas with only scattered trees. Thus, the rainforests of the isthmus are characterized by a much higher relative humidity than are the savannas or semi-arid scrub forests. Although with regard to rainfall there is a pronounced dry season in the regions supporting rainforest, there still remains considerable atmospheric moisture in this environment throughout the year. The dense foliage provides shade and protection from desiccating effects of wind and sunlight; furthermore the foliage contributes moisture by transpiration. The deep alluvial soils mixed with large quantities of organic matter (decaying leaves and rotting logs) maintain considerable quantities of moisture.

Conversely, the savannas and scrub forests have little atmospheric moisture during the dry season. In the former habitat there are few trees to provide shade or moisture through transpiration; in the latter most of the trees lose their leaves during the dry season. Thus, these environments are desiccated by the dry winds and direct sunlight. Furthermore, the soils in these environments become dry and caked. There is little or no terrestrial matter to hold moisture.

Free water in these environments is present in a variety of forms

at different times of the year. During the dry season the more extensive marshes in the savannas persist; many ponds and most of the streams in the rainforest are permanent throughout the year. In the scrub forest all except the largest streams become dry during the dry season, and no ponds exist through the dry season. With the advent of the first heavy summer rains the stream beds fill with water, marshes expand, and many depressions become ponds (Pl. 5, fig. 2). At this time the amount of free water in the scrub forests and savannas greatly increases, much more so than that in the rainforests.

Environments are vertically stratified in the rainforests. There is the deep alluvial soil, the ground litter of leaves and decaying logs, the low bushes and small trees, and finally the tall trees of the forest. Each of these provides certain types of shelter for amphibians. The moist soil and litter on the forest floor is an important microhabitat for fossorial and strictly terrestrial species. The dense foliage of the trees, tree holes, and bromeliads growing on the trees provide shelter for arboreal species. Arboreal and terrestrial bromeliads and the terrestrial elephant-ear plants (*Xanthosoma*) contain water in the axils of their leaves throughout the year and thus provide an important habitat for amphibians. The low, spiny, deciduous trees of the scrub forest and the grasses and scattered trees in the savannas provide little shelter. In the savannas there are depressions, some of which contain water throughout the year; these are often surrounded by trees providing refugia for amphibians during the dry season. In the scrub forest many species congregate along streams and in moist stream beds during the dry season.

Now that the important ecological factors of the major environments have been outlined, we may examine the local distribution of amphibians in each of these. Beginning with the rainforest, we find only one fossorial species, *Gymnopis mexicanus*. A large number of species are found on the forest floor; characteristic inhabitants of the leaf litter are: *Bufo valliceps, Eleutherodactylus rhodopis, Microbatrachylus pygmaeus,* and *Syrrhophus leprus*. Other terrestrial amphibians usually are not scattered throughout the rainforest, as are those named immediately above, but instead inhabit areas of forest adjacent to ponds or streams; these species include: *Bufo marinus, Eleutherodactylus natator, Eleutherodactylus rugulosus, Leptodactylus labialis, Leptodactylus melanonotus, Rana palmipes* and *Rana pipiens*. The most striking ecological assem-

blage of amphibians in the rainforest is the arboreal group of species, including:

Bolitoglossa occidentalis
Bolitoglossa platydactyla
Eleutherodactylus alfredi
Hyla baudini
Hyla ebraccata
Hyla loquax
Hyla microcephala martini
Hyla picta
Phrynohyas modesta
Phrynohyas spilomma
Phyllomedusa callidryas taylori

In the savannas *Rhinophrynus dorsalis, Engystomops pustulosus,* and *Gastrophryne usta* are fossorial species. *Bufo marinus, Leptodactylus melanonotus, Leptodactylus labialis, Rana palmipes,* and *Rana pipiens* are found in the vicinity of permanent water in the savannas. Although the savanna habitat does not provide the ecological conditions for the existence of an arboreal fauna, many arboreal species from the surrounding rainforest utilize the extensive marshes and ponds in the savannas for breeding purposes. Thus, *Hyla baudini, Hyla microcephala martini, Hyla picta,* and *Phrynohyas spilomma* have been found breeding in savannas. In parts of savannas where clumps of trees surround depressions containing water throughout the year, individuals of the species named above, together with *Hyla loquax* and *Phyllomedusa callidryas taylori,* may not only breed, but remain throughout the year.

In the semi-arid scrub forest the same fossorial species as exist in the savannas are found. Likewise, *Bufo marinus, Leptodactylus labialis, Leptodactylus melanonotus,* and *Rana pipiens* are found near permanent water. Terrestrial species in this semi-arid environment include *Bufo canaliferus, Bufo coccifer, Bufo marmoreus, Syrrhophus pipilans,* and *Diaglena reticulata.* Of these, *Syrrhophus pipilans* sometimes inhabits low trees and bushes; the others may be fossorial. The arboreal species in the scrub forest include *Hyla baudini, Hyla robertmertensi, Hyla staufferi,* and *Phyllomedusa dacnicolor.*

Eleutherodactylus rugulosus and *Hylella sumichrasti* live along streams in the scrub forest. *Hylella sumichrasti* lays its eggs in these streams.

In comparing the ecological differences in the amphibian assemblages in the three major habitats, the most obvious difference is the great percentage of arboreal species in the rainforest as compared with savanna and scrub forest. Only four arboreal species are found in the scrub forest, none in the savannas, but eleven in the rainforest. Likewise, there is an absence of ground-dwelling forms in the arid habitats; in the latter the only terrestrial

species are those that are found near water. A possible exception is *Syrrhophus pipilans.*

From the above analysis of ecological distribution we may see that the rainforest provides a variety of habitats for amphibians and that these habitats are suitable for amphibian life throughout the year. On the other hand, the savannas and scrub forests are characterized by extreme conditions of desiccation, a factor of considerable importance in limiting the ecological distribution of amphibians. However, there still is a diversity of amphibians in these semi-arid environments. Obviously, these species are adapted in various ways for survival during the dry season, at which time environmental conditions are such that the animals cannot carry on their normal activities.

Although there is not an abundance of data concerning the seasonal activity of the fauna, what is available shows some interesting correlations with the environments. During the dry season in the scrub forest there is essentially no amphibian activity; an occasional *Rana pipiens* may be seen along a river, or a *Bufo marinus* may be seen at night. In the rainforest the terrestrial-breeding amphibians are active during the dry season. *Eleutherodactylus rugulosus* is found at night or by day along streams. *Eleutherodactylus rhodopis, Microbatrachylus pygmaeus,* and *Bufo valliceps* are active during the day; these plus *Bolitoglossa occidentalis, Bolitoglossa platydactyla, Eleutherodactylus alfredi, Eleutherodactylus natator,* and an occasional *Hyla* are active at night.

With the onset of the heavy summer rains and the subsequent formation of breeding ponds, amphibian activity reaches a peak. This is especially noticeable in the semi-arid environments, where during the dry season there is little activity.

Among the anurans in the isthmus the four species of *Eleutherodactylus,* the two species of *Syrrhophus,* and the one species of *Microbatrachylus* are either known, or presumed, to lay eggs on the ground; these develop directly into small frogs. All of the other anurans deposit their eggs in water or attach them to objects over water (*Phyllomedusa*); these hatch into tadpoles, which later metamorphose into frogs. *Hylella sumichrasti* is known to breed only in streams. All of the other species breed in ponds, but at times some species deposit their eggs in streams; in this last group are *Bufo valliceps, Bufo marmoreus, Phyllomedusa callidryas taylori,* and *Rana pipiens.*

Although the ecological data are incomplete, they do show that

ecological conditions differ greatly in the three major environments, different species of amphibians inhabit these environments, and that the fauna is ecologically diversified in each environment.

Distribution of the Fauna

Plotting the distributions of species of amphibians known to live in the lowlands of the Isthmus of Tehuantepec results in an array of geographic patterns. These may be analyzed with respect to those species that are restricted either to the Gulf lowlands or the Pacific lowlands, or those that occur on both the Gulf and Pacific lowlands. Furthermore, the distributions may be analyzed with respect to those species whose ranges extend from México across the Isthmus of Tehuantepec into Central America, those that reach the isthmus from Central America but do not extend into México proper, and those that reach the isthmus from México but do not extend into Central America. It should be kept in mind that the following analysis is of the lowland inhabitants only. Species inhabiting the foothills and mountains will be discussed later.

1. SPECIES RESTRICTED TO THE GULF LOWLANDS. Of the 36 species of amphibians recorded from the Isthmus of Tehuantepec, nine (25 per cent) are in this group. Four of these (*Eleutherodactylus alfredi, Syrrhophus leprus, Hyla loquax,* and *Hyla picta*) live in the Gulf lowlands to the east and to the west of the isthmus. Three others (*Hyla ebraccata, Hyla microcephala martini* and *Phyllomedusa callidryas taylori*) are primarily Central American in their distribution and reach the northwestern limits of their ranges in the Gulf lowlands of the isthmus, whereas *Bolitoglossa platydactyla* and *Eleutherodactylus natator* reach the southern limits of their distributions in the isthmus.

2. SPECIES RESTRICTED TO THE PACIFIC LOWLANDS. This group includes six species, or 17 per cent of the amphibian fauna of the isthmus. Two of these (*Bufo coccifer* and *Syrrhophus pipilans*) range to the east and to the west of the isthmus on the Pacific lowlands. Two others (*Bufo canaliferus* and *Hyla robertmertensi*) range from the isthmus into Central America, and *Diaglena reticulata* and *Phyllomedusa dacnicolor* range on the Pacific lowlands of México southeastward to the isthmus.

3. SPECIES THAT OCCUR ON THE PACIFIC AND GULF LOWLANDS. This group includes 19 species, or 53 per cent of the total amphibian fauna. Of these, nine species (25 per cent of the entire amphibian

fauna) are widespread throughout the lowlands of México and Central America; these are:

Gymnopis mexicanus
Rhinophrynus dorsalis
Bufo marinus
Engystomops pustulosus
Leptodactylus labialis
Leptodactylus melanonotus
Hyla baudini
Hyla staufferi
Rana pipiens

Four species occur on the Gulf lowlands to the east and to the west of the isthmus, but on the Pacific lowlands they occur only to the east; this group includes *Bufo valliceps, Eleutherodactylus rhodopis, Phrynohyas modesta,* and *Phrynohyas spilomma.* Three species live to the east and to the west of the isthmus on the Pacific lowlands, but only to the west on the Gulf lowlands; these include *Eleutherodactylus rugulosus, Microbatrachylus pygmaeus,* and *Gastrophryne usta.*

Six species that cross the isthmus live on the humid Gulf lowlands and on the humid lowlands of Chiapas and Guatemala, but not on the semi-arid Plains of Tehuantepec; these include *Bolitoglossa occidentalis, Eleutherodactylus rhodopis, Microbatrachylus pygmaeus, Phrynohyas modesta, Phrynohyas spilomma,* and *Rana palmipes.* Of these, *Microbatrachylus pygmaeus* also occurs in scattered humid environments to the west of the isthmus on the Pacific lowlands.

Two species are endemic to the isthmian region. *Bolitoglossa veracrucis* is known only from the humid northern slopes of the isthmus. *Hylella sumichrasti* occurs on the Pacific slopes of the isthmus and extends to the east into western Chiapas.

In analyzing the distribution of the amphibians with respect to those that are restricted to either the Pacific or Gulf lowlands or those that cross the continental divide in the isthmus, we find that 25 per cent of the species are restricted to the Gulf lowlands, 17 per cent are restricted to the Pacific lowlands, and 53 per cent cross the isthmus. In analyzing the distribution patterns with respect to those that extend across the isthmus of Tehuantepec from east to west, we find that 14 per cent of the species do not extend east of the isthmus into Central America and that 19 per cent do not range west of the isthmus into México proper; 61 per cent of the species range to the east and to the west of the isthmus. Of the 36 species of amphibians inhabiting the isthmus only nine species (25 per cent) range across the isthmus, that is, occur on the Gulf and Pacific lowlands, and also range to the east and to the west of the isthmus. To these wide-ranging species the diversified environments of the

isthmus do not present a barrier to distribution. The other 27 species (75 per cent) either do not cross the isthmus from east to west or from north to south; thus, probably in one way or another the isthmus presents a barrier to their distribution.

THE AMPHIBIAN FAUNA OF THE FOOTHILLS AND ADJACENT HIGHLANDS

To amphibians inhabiting the foothills and mountains of southern México and northern Central America, the isthmus presents a great barrier to dispersal. For example, salamanders of the genus *Thorius*, the *mexicanus* and *augusti* groups of the genus *Eleutherodactylus*, the *bistincta* group of the genus *Hyla*, and the genus *Tomodactylus* occur on the Mexican Plateau and southward into the mountains of Oaxaca. Nevertheless, no members of these groups are present in the Guatemalan-Chiapan Highlands. The genera *Chiropterotriton*, *Magnadigita*, *Pseudoeurycea*, and *Ptychohyla*, as well as the *eximia* group of *Hyla* are represented by different species in the Guatemalan-Chiapan Highlands than in the mountains of México on the other side of the isthmus. Several species of *Plectrohyla* occur in the Guatemalan-Chiapan Highlands, but none is known from the Mexican Highlands, although one species occurs in the Tuxtlas.

Living in the humid forests of the foothills are salamanders of the genus *Lineatriton*, frogs of the *spatulatus* group of *Eleutherodactylus*, *Anotheca coronata*, *Hyla miotympanum*, and *Phyllomedusa moreleti*. All of these occur in the foothills of the Sierra Madre Oriental in eastern México and in Los Tuxtlas. *Lineatriton*, *Hyla miotympanum*, and the *spatulatus* group of *Eleutherodactylus* do not occur in the foothills of the Guatemalan-Chiapan Highlands; those amphibians reach the end of their ranges at the isthmus. *Phyllomedusa moreleti* and *Anotheca coronata* are found in the northern foothills of the Guatemalan-Chiapan Highlands, and *Phyllomedusa moreleti* is found in the foothills on the Pacific slopes of the Chiapan Highlands.

Although the above analysis is not so detailed as that of the lowland inhabitants, it does show that all of the genera and species of amphibians known to inhabit the foothills and highlands adjacent to the isthmus, only two species of amphibians cross the isthmus from one highland mass to the other. Thus, it is evident that the Isthmus of Tehuantepec presents a great barrier to dispersal of these groups of amphibians.

ESTABLISHMENT OF PRESENT PATTERNS OF DISTRIBUTION

From the foregoing analysis of geographical and ecological distribution in the Isthmus of Tehuantepec we may strive for an interpretation of the events that led to the establishment of patterns of distribution displayed not only by the amphibians, but other terrestrial vertebrates as well. The thesis that I am proposing below is based on the premise that in southern México and northern Central America climatic fluctuation during the Pleistocene was of sufficient magnitude to cause vegetational shifts, both vertically and latitudinally, resulting in the establishment of alternating continuous and discontinuous lowland and highland environments, although this climatic fluctuation was not so great as to eliminate tropical lowland environments from the region. I feel that the present patterns of distribution of the amphibians in the Isthmus of Tehuantepec may be explained on this premise.

Many authors dealing with the herpetofauna of Middle America have followed Schuchert's (1935) suggestion of a seaway in the isthmus during the Cenozoic. Thus, Burt (1931), Duellman (1956, 1958a), Gloyd (1940), Oliver (1948), Smith and Laufe (1946), and Stuart (1941) employed the presence of a seaway to explain distribution and speciation in various genera. Durham, Arellano, and Peck (1952), Olson and McGrew (1941), and Stirton (1954) have provided geological evidence that there probably was no Cenozoic seaway in the Isthmus of Tehuantepec. Even if there were a seaway in the Pliocene or Miocene (the dating of this possible seaway is open to question), its presence is not necessary to explain the present patterns of distribution in the isthmus.

In recent years the study of natural biotic environments, palynology, and Pleistocene chronology in Middle America has produced a wealth of data, which although still fragmentary begins to form a picture of past climatic events in that part of the world. Sedimentary studies by Hutchinson, Patrick, and Deevey (1956) and Sears, Foreman, and Clisby (1955) have provided evidence of drastic climatic shifts in México during the Pleistocene. Further evidence of bioclimatic fluctuation is provided by Martin and Harrell (1957) and Martin (1958); the latter has suggested that there was a displacement of the tropical zones in southern México and northern Central America by as much as 3000 feet during the glacial maximum. Much of the evidence of such drastic vertical

shifts in environments is based on the presence of Pleistocene montane glaciers on Mexican volcanoes (White, 1956) and Chirripo in Costa Rica (Weyl, 1955). Dorf (1959) supports this idea of drastic climatic change.

In his studies of the avifauna of México and Guatemala Griscom (1932 and 1950) made an important issue of the continuity of the bird fauna in what he called the Subtropical Life-zone, which essentially consists of cloud forest, a widespread, but discontinuous, habitat on the Gulf (windward) slopes of the Mexican and Central American highlands at elevations between 1000 and 2000 meters. To account for this apparent uniformity in the avifauna Griscom hypothesized a continuity of cloud forest environment in the Pleistocene; this would result in the depression of cloud forests to the coastal lowlands and the displacement of tropical lowland environments far to the south in Central America. Stuart (1951) objected to this displacement of lowland tropical rainforest; he stated that a descent to sea level of a subtropical zone would have brought about either widespread extermination of the tropical fauna or acclimatization of that fauna to subtropical conditions.

Although palynological studies and some faunal studies of subtropical and temperate animals suggest a drastic climatic fluctuation that might have eliminated tropical environments in southern México and northern Central America, there is much biological evidence indicating the existence of tropical environments in this region even during the glacial maximum. Especially significant is the diversity of species inhabiting the present tropical environments; many of these have differentiated from related taxa to the south.

In the Pleistocene, climate fluctuated and vegetation shifted correspondingly in southern México and northern Central America. Most of the palynological studies and many studies of Pleistocene chronology deal with montane regions, either the Mexican Plateau or the mountains rising from the plateau. No such studies have been made in lowland tropical environments. During glacial advances the tropical lowland environments in México probably were not eliminated, for the great diversity of animals in these environments supports the hypothesis that they have been in existence for some time, although periodically they may have been discontinuous.

In order to understand the nature of bioclimatological events in the Pleistocene in lowland tropical environments of southern México, certain factors that are of little importance in the interpreta-

tion of Pleistocene chronology in the highlands must be considered. These factors are: 1) climatic moderation by oceans, 2) fluctuation in sea level, and 3) fluctuation in level of the water table as affected by sea level.

It is well-known that large bodies of water moderate the temperature on adjacent land. Furthermore, it is kown that faunas of marine invertebrates shifted latitudinally in the Pleistocene; Trask, Phleger, and Stetson (1947) recorded cold-water Foraminifera then as far south as the Sigsbee Deep in the middle of the Gulf of Mexico. Large bodies of warm water, such as the Gulf of Mexico, Caribbean Sea, and Pacific Ocean of today, probably were not sufficiently cooled at the time of glacial advance to affect greatly the temperature of the winds blowing across them. Even if these bodies of water were somewhat cooler than now, the prevailing winds blowing from them onto the lowlands of México and northern Central America would have aided in maintaining relatively high temperatures there. These warm winds probably counteracted the cooling effect of glaciation in the lowlands and thereby maintained tropical conditions near the seas.

Although no adequate studies of Pleistocene beach lines have been made in southern México, such information is available for peninsular Florida on the other side of the Gulf of Mexico (Cooke, 1945). Fluctuation in sea level in the Pleistocene has been used by Hubbell (1954), Goin (1958), and Duellman and Schwartz (1958) to explain present patterns of distribution of animals in Florida. If Cooke's interpretations can be applied to the western side of the Gulf of Mexico, even generally, it would be supposed that sea level varied from about 300 feet lower than at present during the Illinoian Glacial Period to about 275 feet higher than at present during the Aftonian Interglacial Period. Lowering of sea level would expand the lowlands in the isthmus; rising sea level would restrict them, leaving only the central ridges and many islands in the isthmus, but never forming a seaway between the Gulf of Mexico and the Pacific Ocean.

Probably the level of the water table in the coastal lowlands and the gradients of the streams in the lowlands and foothills was closely correlated with fluctuation in sea level. If sea level fluctuated as much as 575 feet in the Pleistocene, changes in the level of the water table must have been of considerable magnitude.

During times of glacial advances the lowlands of the isthmus probably were more extensive and had more semi-arid tropical

environments than at present, with patches of rainforest existing in sheltered valleys along the major streams. In the course of bioclimatic fluctuation the semi-arid environments (scrub forest and/or savanna) were continuous at times from the Pacific lowlands across the isthmus to the Gulf lowlands. At those times such typical inhabitants of the semi-arid environments as *Rhinophrynus dorsalis, Engystomops pustulosus,* and *Hyla staufferi* could have made their way across the isthmus. At times of most extensive glaciation, such as the Illinoian, temperatures in the isthmus probably were low enough to permit the growth of pine-oak forest and cloud forest continuously across the central ridges from the Mexican to the Chiapan-Guatemalan highlands. At those times such highland members of the fauna as *Chiropterotriton, Pseudoeurycea, Magnadigita,* and the *eximia* group of *Hyla* could have crossed the isthmus. During Wisconsin time, climate probably fluctuated less than during previous glaciations; probably no montane environments, except cloud forest, were represented in the isthmus during the Wisconsin. Even at this relatively late date such animals as *Lineatriton lineola, Anotheca coronata,* and *Phyllomedusa moreleti* could have crossed the isthmus.

During the interglacial periods, which in the isthmian region were characterized by warmer temperatures, higher sea level and consequently more restricted areas of lowlands, and possibly more rainfall than in the glacial periods, the continuity of pine-oak forest and cloud forest from east to west across the isthmus was interrupted. Probably, too, the semi-arid environments were restricted, and the rainforests were more widespread. At those times animals now inhabiting the rainforests of the Gulf lowlands and those inhabiting the Pacific lowlands of Chiapas and Guatemala could have crossed the isthmus. In this group are species such as *Bolitoglossa occidentalis, Eleutherodactylus rhodopis, Microbatrachylus pygmaeus,* and *Rana palmipes.*

The amount of differentiation in isolated populations of amphibians in southern México and northern Central America gives some idea of relative lengths of time of isolation from related populations. Those populations inhabiting high mountain environments on either side of the isthmus are specifically distinct. Some populations inhabiting cloud forests lower on the mountains are specifically distinct from related populations on the other side of the isthmus; between others there is no recognizable differentiation. Even though many populations are isolated from other populations of the same species in the lowlands of the isthmus, there is

no apparent speciation. This indicates that the lowland environments and their inhabitants have been isolated from one another for a shorter time than have the highland environments and their inhabitants.

ACCOUNTS OF SPECIES

For each species of amphibian known to occur in the lowlands of the Isthmus of Tehuantepec, localities where one or more specimens were collected are listed, and variation, ecology, and life histories are discussed. A total of 2833 specimens has been examined for the purposes of this study. Individual specimens cited in the text are listed with catalogue numbers and abbreviations of the name of the museum, as follows:

AMNH	American Museum of Natural History
KU	University of Kansas Museum of Natural History
MCZ	Museum of Comparative Zoology, Harvard College
UIMNH	University of Illinois Museum of Natural History
UMMZ	University of Michigan Museum of Zoology
USNM	United States National Museum

Gymnopis mexicanus mexicanus Duméril and Bibron

Oaxaca: El Barrio (3); Matías Romero; Tehuantepec (2). *Veracruz:* Cosamaloapan; Cuatotolapam (2).

The two specimens from Cuatotolapam were collected by Ruthven in an area of mixed savanna and forest. The three specimens (USNM 30535-7) listed above from El Barrio were collected by Sumichrast; possibly they came from another locality. The city of Tehuantepec is divided into seven districts called "barrios." The two specimens listed from Tehuantepec (MCZ 1604) merely bear the data "Tehuantepec, Mexico." They may have come from the town, the district, or from anywhere in the isthmus. The specimen from Matías Romero has 109 primary and 67 secondary annuli, a length of 400 mm., and a diameter of 19 mm.; the one from Cosamaloapan has 106 primary and 58 secondary annuli, a length of 397 mm., and a diameter of 19 mm. Data on the other specimens were recorded by Dunn (1942:475).

Bolitoglossa occidentalis Taylor

Oaxaca: Río Sarabia (2); Ubero. *Veracruz:* La Oaxaqueña; 14 km. E of Suchil.

The specimens from Oaxaca are only tentatively assigned to *occidentalis.* All are immature and lack maxillary teeth. Taylor (1941:147) stated that the maxillary teeth are absent in young *occidentalis.* One from Río Sarabia is a male with a body-length of 29 mm. and a tail-length of 22 mm. The dorsum is reddish brown

streaked with dark gray; the venter is dark gray. Two small individuals (one from Sarabia and one from Ubero) have body-lengths of 19 and 21 mm. and tail-lengths of 10.5 and 11 mm. In life they were pale yellowish tan above with a brown triangular mark on the occiput, but with no middorsal stripe. Both were found in the axills of elephant ear plants (*Xanthosoma*).

This species has been noted by Goodnight and Goodnight (1956: 146) on the Atlantic lowlands at Palenque, Chiapas, and by Shannon and Werler (1955:362) at several localities in Los Tuxtlas, Veracruz. I have collected it at Vista Hermosa on the eastern slopes of the Sierra Madre Oriental above Tuxtepec in northern Oaxaca. Both *B. occidentalis* and *B. rufescens* have been reported from Palenque, Chiapas (Taylor and Smith, 1945:547). Reëxamination of specimens from northern Chiapas and Tabasco is needed to verify the sympatric occurrence of these two similar species.

Bolitoglossa platydactyla Tschudi

Oaxaca: La Oaxaqueña; Tolosita (2). *Veracruz:* Acayucan; Cuatotolapam; 25 km. ESE of Jesús Carranza; 14 km. E of Suchil; 2.7 km. N of Tula.

Known only from the Gulf lowlands in the isthmian region, this species has been taken in a variety of habitats within the humid forest area: under outer leaves of banana plants, under a rock along a stream, under a log in a plowed field, and on a reed in a pond at night. Three adult males have an average snout-vent length of 44 mm. and a tail-length of 41 mm. In life the color of the dorsum varied from orange-yellow to orange-tan, usually being more orange on the tail. The iris was a reddish orange.

Bolitoglossa veracrucis Taylor

Veracruz: 35 km. SE of Jesús Carranza (21).

This species is known only from the type series collected at night on a limestone cliff by Walter W. Dalquest. If this salamander is restricted to this type of habitat, it should be found in the region of extensive limestone outcroppings in northern Chiapas and southern Tabasco.

Rhinophrynus dorsalis Duméril and Bibron

Oaxaca: Ixtepec; Limón; Salina Cruz (18); Tehuantepec (57); Tuxtepec (3). *Veracruz:* Amatitlán (3); Cosamaloapan (5); Novillero (2); San Lorenzo.

This species inhabits the scrub forests of the Pacific coastal plain and the savannas in southern Veracruz; apparently it does not occur in rainforest. Consequently, its distribution in the isthmus is discontinuous.

PLATE 1

FIG. 1. Savanna about 75 kilometers east of Coatzacoalcos, Veracruz. Photograph by L. C. Stuart.

FIG. 2. Low scrub forest near Alvarado, Veracuz. Photograph by L. C. Stuart.

PLATE 2

FIG. 1. Rainforest near Tolosita, Oaxaca. March, 1956.

FIG. 2. Rainforest along the Río Sarabia, Oaxaca. March, 1956.

PLATE 3

FIG. 1. Transition forest near La Princesa, Oaxaca. March, 1956.

FIG. 2. Palm Savanna on the Plains of Chivela, Oaxaca. March, 1956.

PLATE 4

FIG. 1. Scrub forest on the Plains of Tehuantepec in dry season. March, 1936.

FIG. 2. Scrub forest on the Plains of Tehuantepec in rainy season. View toward the north. In the distance is the Continental Divide in the hills of the Isthmus. July, 1938.

PLATE 5

FIG. 1. Low, dense scrub forest near La Ventosa, Oaxaca. July, 1958.

FIG. 2. Temporary pond in scrub forest north of Salina Cruz, Oaxaca. July 7, 1958. *Rhinophrynus dorsalis*, *Bufo marmoreus*, and *Diaglena reticulata* were breeding here the previous night.

PLATE 6

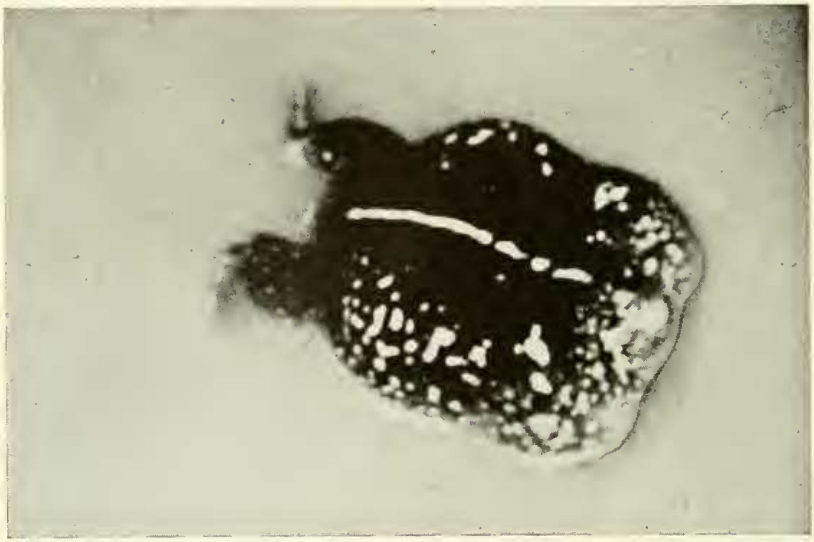

FIG. 1. Calling male of *Rhinophrynus dorsalis*, photographed in a pond north of Santa Cruz, Oaxaca, on July 6, 1958. × ⅔.

FIG. 2. Color pattern variation in two adults of *Bufo canaliferus* from Juchitán, Oaxaca. × ⅔.

PLATE 7

FIG. 1. Calling male of *Engystomops pustulosus*, photographed in a pond west of Tehuantepec, Oaxaca, on July 5, 1956. × 2.

FIG. 2. Foamy egg mass of *Engystomops pustulosus* at the edge of a pond west of Tehuantepec, Oaxaca. July 5, 1956. × ⅜.

PLATE 8

FIG. 1. Calling male of *Diaglena reticulata*, photographed at a pond north of Salina Cruz, Oaxaca, on July 6, 1958. × ½.

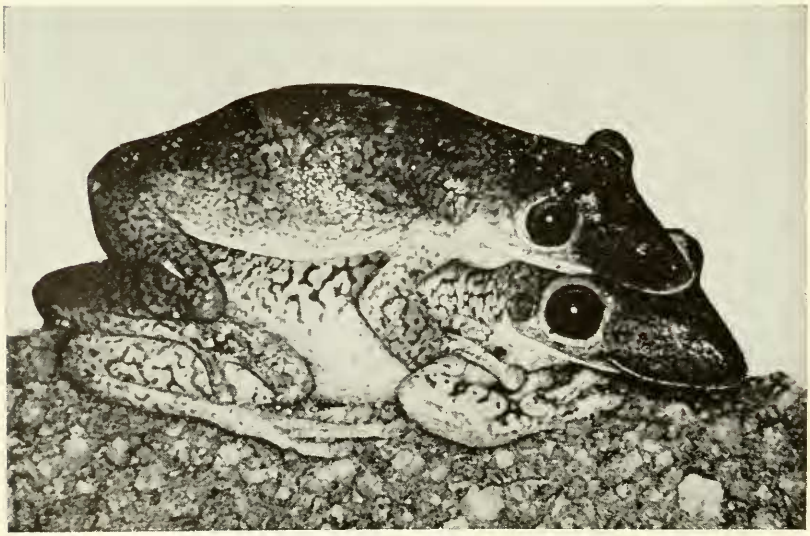

FIG. 2. Clasping pair of *Diaglena reticulata* at the edge of a pond north of Salina Cruz, Oaxaca, on July 6, 1958. × 1.

Breeding congregations were found after heavy rains at Tehuantepec on July 5, 1956, at Cosamaloapan, Novillero, and Amatitlán on July 26, 1956, and at Salina Cruz on July 6, 1958. The call is a long "worrp" made while the male is floating on the surface of the pond. The small heads, small limbs, and greatly inflated bodies cause the calling males to resemble miniature caricature balloons (Pl. 6, fig. 1). Amplexus is inguinal. These toads are notably wary, even when calling. Often the beam of a flashlight or the slightest disturbance of the water will cause the males to stop calling. The body is deflated with one last nauseous note, and the frog sinks beneath the surface of the water and swims away with short slow kicks of the hind feet.

Bufo canaliferus Cope

Oaxaca: Chivela; Salina Cruz; Santa Efigenia; Tapanatepec (6); Tehuantepec (10); Zanatepec (4).

This small toad apparently is restricted to the Pacific lowlands from the Isthmus of Tehuantepec eastward to Guatemala. At Zanatepec on July 13, 1956, males were calling from a flooded field bordered by scrub forest. The call is a rather loud nasal racket. Living individuals vary greatly in coloration. Some have yellowish tan flanks and dorsum and an orange middorsal stripe; others have a pale red dorsum, yellow flanks, and a cream middorsal stripe (Pl. 6, fig. 2).

Bufo coccifer Cope

Oaxaca: Juchitán (5); Tehuantepec.

It is with some degree of hesitancy that these toads are referred to the species *coccifer*. Although these and other specimens from Guerrero and Michoacán display no striking differences from specimens from Costa Rica, Nicaragua, and southeastern Guatemala, the ranges of the populations are separated by a broad hiatus in Chiapas and Guatemala. Possibly this species has utilized the sub-humid corridor through northern Central America (Stuart, 1954) and subsequently disappeared from the corridor in Guatemala and Chiapas. Specimens of a *coccifer*-like toad collected by Stuart in the vicinity of Jacaltenango, Departamento Huehuetenango, Guatemala, are much larger than either the Central American or Mexican specimens of *coccifer*. A final commitment on the systematic status must await a thorough study of this group of toads.

Males of this species were calling from a grassy rain-pool in open scrub forest at the edge of Juchitán on July 6, 1956. The call is a low

"whirrr." The calling males were sitting in the shallow water at the edge of pond, where they were hidden by the grass. None was observed in open water, as is characteristic of calling males of *Bufo canaliferus* and *marmoreus*.

Bufo marinus Linnaeus

Oaxaca: Agua Caliente; Guichicovi (3); Mixtequilla; Tolosita (6); Tehuantepec (37); Tuxtepec; Unión Hidalgo. *Veracruz:* Ciudad Alemán (4); Cosamaloapan; Cuatotolapam (19); 20 km. SE of Jesús Carranza (4); 38 km. SE of Jesús Carranza (10); 20 km. NE of Jesús Carranza (4); Novillero.

This large toad is abundant throughout the lowlands of the isthmus. The loud rattling call of males was heard on rainy nights throughout the summer. In March, 1956, several adults were found in a small cave back of a spring at Agua Caliente.

Bufo marmoreus Wiegmann

Oaxaca: Cerro San Pedro (2); Chivela (5); Escurano (3); Juchitán; Salina Cruz (101); Santa Lucía (2); 12 km. S of Santiago Chivela (11); Santo Domingo; Tapanatepec; Tehuantepec (100); Tequisistlán. *Veracruz:* Alvarado; Coatzacoalcos.

This toad is abundant on the Pacific lowlands, where it inhabits both open and dense scrub forest. On the Gulf lowlands its distribution seems to be limited to xeric coastal habitats. Aside from the specimens from Alvarado and Coatzacoalcos, it is known in Veracruz only from Boca del Río (Langebartel and Smith, 1959:27).

The similarity in size of *Bufo marmoreus* and *valliceps* and their almost completely allopatric ranges suggest that the two species may be in competition at any one locality. Nevertheless, both were calling from a small rocky stream south of Santiago Chivela on July 6, 1956.

On the night of July 6, 1958, an estimated 400 toads of this species made up a breeding congregation near Salina Cruz. The site was a shallow muddy pond about 20 x 40 meters located in an area cleared of scrub forest; the banks of the pond were devoid of vegetation (Pl. 5, fig. 2). Breeding in the same pond were *Rhinophrynus dorsalis* and *Diaglena reticulata*. The following morning no more than a dozen *Bufo* were found in the pond, but several individuals were found beneath debris and in small burrows near the pond. On July 7, 1958, large numbers of tadpoles and recently metamorphosed young were in a shallow grassy pool just east of Salina Cruz.

Taylor (1943b:347) referred certain specimens from Tehuantepec to *Bufo perplexus,* a species closely related to *Bufo mar-*

moreus. Evidence to be presented elsewhere shows that *perplexus* does not occur in the isthmus.

Bufo valliceps valliceps Wiegmann

Oaxaca: Guichicovi (2); Matías Romero; 32 km. N of Matías Romero (2); Nueva Raza; Río Sarabia (3); Santa María Chimalapa (14); Santiago Chivela; 12 km. S of Santiago Chivela (5); Santo Domingo (5); Tolosita (7). *Veracruz:* Acayucan (3); Alvarado; Amatitlán; Ayentes; Cosamaloapan (3); Cosoleacaque (6); Cuatotolapam (14); Hueyapan; 20 km. ENE of Jesús Carranza (6); 20 km. S of Jesús Carranza; 25 km. SE of Jesús Carranza (23); 35 km. SE of Jesús Carranza; 60 km. SW of Jesús Carranza (5); La Oaxaqueña (4); Novillero (4); San Lorenzo (5).

Individuals were found in both wet and dry seasons. In the dry season they were most frequently found in rainforest, whereas in the rainy season breeding congregations were found in savannas as well. This toad occurs throughout the Gulf lowlands and on the Pacific slopes and in the Grijalva Valley of Chiapas and Guatemala, but not on the Pacific lowlands of the isthmus.

I have not been able to recognize individuals referrable to the race *macrocristatus*. Firschein and Smith (1957:219) described *macrocristatus* from the mountains of eastern Oaxaca and referred to it specimens from the Gulf lowlands of northern Chiapas. None of the present material shows the hypertrophied cranial crests supposedly characteristic of *macroaristatus*, nor do specimens from the isthmus resemble the population in the Grijalva Valley being described by L. C. Stuart, who will discuss the variation in, and the valadity of, the named populations of *valliceps*.

Five specimens from San Lorenzo, Veracruz (USNM 123516-20), were identified as *Bufo cristatus* by Smith (1947:408). Firschein (1950: 83) redefined the *cristatus* group of *Bufo* and assigned these specimens to *valliceps*.

Eleutherodactylus alfredi Boulenger

Oaxaca: Tolosita (2). *Veracruz:* 35 km. SE of Jesús Carranza (6).

These specimens were collected in rainforest. Shreve (1957: 247) pointed out the close resemblance between *E. alfredi* and *E. conspicuus* from Piedras Negras, Guatemala, and treated them as subspecies. Examination of the specimens from the isthmus, together with seven from central Veracruz and one from Teapa, Tabasco, suggests an even closer relationship. *Eleutherodactylus conspicuus* was diagnosed by Taylor and Smith (1945:567) as differing from *alfredi* "in lacking a tarsal fold, in having shorter hind legs with the tibiotarsal articulation reaching only to the nostril instead of beyond the tip of the snout; the vomerine teeth barely reach the posterior level of the choanae." The specimen from

Teapa has the vomerine teeth reaching to the posterior edge of the choanae; in the eight specimens from the isthmus the teeth reach the posterior edge of the choanae in two and to the middle of the choanae in six; in seven specimens from central Veracruz the teeth reach the posterior edge of the choanae in two and to the middle in five. The tibiotarsal articulation extends beyond the tip of the snout in the specimen from Teapa and in two from central Veracruz; in three specimens from the isthmus and in one from central Veracruz it extends only to the nostril; in the others it extends to the snout. The tarsal fold is absent in the specimen from Teapa, in three from the isthmus, and in all those from central Veracruz; it is weakly present in the others.

In the light of this evidence there seems to be little justification in recognizing two species or even two subspecies in this group. Consequently, *Eleutherodactylus conspicuus* Taylor and Smith (1945) is here placed in the synonymy of *Eleutherodactylus alfredi* Boulenger (1898), a species with a range extending from Cuautlapan and Potrero Viejo in central Veracruz southward and eastward in forested habitats to western El Petén, Guatemala.

Eleutherodactylus natator Taylor

Veracruz: 35 km. SE of Jesús Carranza (3); 38 km. S of Jesús Carranza; 55 km. SE of Jesús Carranza.

The snout-vent length is 42.0 mm. in a male and averages 59.5 mm. in three adult females. The tarsal fold is low and extends about half the length of the tarsus; the first and second fingers are subequal in length; the tibiotarsal articulation extends beyond the tip of the snout. The patches of vomerine teeth lie between the posterior margins of the choanae. The throat and belly are immaculate, and the soles of the feet are dark. In the isthmus this species can be distinguished from *Eleutherodactylus rugulosus* by less rugose skin on the dorsum and absence of dark ventral mottling.

The specimens reported here extend the known range of *natator* eastward from Camotlán, Oaxaca; northward in Veracruz the species inhabits foothills as far north as Huatusco.

Eleutherodactylus rhodopis Cope

Oaxaca: 30 km. N of Matías Romero; Río Sarabia (5); Tapanatepec (87); Tolosita (6); between Zanatepec and Tapanatepec. *Veracruz:* 25 km. SE of Jesús Carranza; 35 km. SE of Jesús Carranza (2); 22 km. SSW of Jesús Carranza; 20 km. ENE of Jesús Carranza (7); Minatitlán; Tapalapan (5).

For the purposes of the present study I am not recognizing *Eleutherodactylus beati, E. dorsoconcolor,* and *E. venustus* as specifically,

or even subspecifically distinct from the earlier named *E. rhodopis.* Probably these are mere color varieties of a single species.

In the dry season frogs of this species were in humid forests, where they were most frequently found along small streams and in ravines. The species is widespread in the Gulf lowlands, but does not occur on the Plains of Tehuantepec. It does inhabit the Pacific slopes on the foothills of the Sierra Madre de Chiapas, the western part of which extends into eastern Oaxaca near Tapanatepec.

Eleutherodactylus rugulosus Cope

Oaxaca: La Princesa (30); Modelo; Santa Lucía (10); Tapanatepec (26); Tehuantepec (6); Tres Cruces (8). *Veracruz:* Tapalapan (5).

In addition to the specimens from the lowlands of the isthmus, for the purposes of the following discussion, I have included data on two specimens from the southern slopes of the Sierra del Sur in Oaxaca (Mirador and Chacalapa) and on several specimens from Los Tuxtlas in Veracruz (Los Chaneques, 67; Salto de Eyipantla, 35; and San Andrés Tuxtla, 11).

Frogs of the *Eleutherodactylus rugulosus* complex occur from southern Veracruz and Sinaloa southward through Central America. Taylor (1940:401) described *E. vocalis* from Hacienda El Sabino, Michoacán; Taylor and Smith (1945:580) described *E. avocalis* from Tres Cruces, Oaxaca. These have been considered as species distinct from *rugulosus,* which is known to occur in Veracruz, Guerrero, and Chiapas southward into Central America. Although the large number of specimens collected in the isthmus does not aid in defining the ranges of the taxa involved, these specimens do give some idea of the variation in certain characters in a given population.

In specimens from Los Tuxtlas the tarsal fold is well-developed and extends two-thirds to three-fourths the length of the tarsus; the tibiotarsal articulation reaches the nostril and sometimes slightly beyond the tip of the snout. In males the tympanum is nearly equal to the diameter of the eye; in females it is about one-half the diameter of the eye. The posterior surfaces of the thighs are dark brown or black with whitish or cream-colored spots, flecks, or irregular mottling. The tarsal fold is dark; the throat is pale in some individuals, but in most is mottled with dark brown or gray flecks. Individuals from La Princesa near the continental divide in Oaxaca show the same variation in body proportions and development of the tarsal fold. The posterior surfaces of the thighs are dark brown in-

distinctly mottled with lighter brown. The throat is dark brown. Specimens from the Pacific slopes of Oaxaca, including the Plains of Tehuantepec, have dark brown thighs mottled with dusty cream. The tibiotarsal articulation extends slightly beyond the tip of the snout in all specimens. In males the tympanum is equal to about two-thirds the diameter of the eye. Duellman (1958b:6) discussed the variation in these characters in populations in Colima, Jalisco, and Michoacán.

Until the extent of variation of these characters is known throughout the range of *rugulosus*, the recognition of populations either as species or subspecies seems superfluous. Consequently, I have used the oldest name; this does not necessarily imply, however, that all populations of *rugulosus (sensu lato)* are conspecific.

Of the 200 specimens examined, 15 have a middorsal stripe that is red or yellow. The iris varies from a copper to a dark golden color and shines bright red at night. Many of the specimens are juveniles; these were collected in the dry season, at which time they were found beneath rocks along streams, in road culverts where there was some water, and in holes in banks and cliffs.

Microbatrachylus pygmaeus Taylor

Oaxaca: La Princesa (5); Matías Romero (9); Río Sarabia (41); Tolosita (2). *Veracruz:* Jesús Carranza; 20 km. ENE of Jesús Carranza.

The specimens listed above vary widely in color patterns; some of the patterns are characteristic of certain named "species": *albolabris, imitator, lineatissimus,* and *minimus.* The large series from the Río Sarabia contains all of the color patterns; this series was obtained in one small ravine in the rainforest. At least in the isthmian region, this species does not inhabit the Pacific slopes and lowlands.

Syrrhophus leprus Cope

Oaxaca: 33 km. N of Matías Romero; Santa Efigenia. *Veracruz:* San Lorenzo.

Although the type locality is stated to be Santa Efigenia on the Pacific slopes of the Sierra Madre de Chiapas in eastern Oaxaca, the type specimen probably came from the northern slopes of the mountains. All other known specimens are from the Gulf slopes and lowlands, and from several localities in Los Tuxtlas. Details concerning specimens from the isthmus and other parts of the range were given by Duellman (1958c:8).

Smith (1947:408) reported a specimen of *Syrrhophus verruculatus* Peters from San Lorenzo, Veracruz; he stated that this speci-

men (USNM 123530) could not be S. *leprus*, because it had a gray belly, nor S. *cystignathoides*, because of the dark and light dorsal coloration. Firschein (1954:57) in his review of the species of *Syrrhophus* in eastern México referred the specimen to S. *cystignathoides*. The specimen is in poor condition. Nevertheless, specific determination is possible. Numerous specimens of S. *leprus* from Los Tuxtlas have gray bellies; some have heavier pigmentation than the specimen from San Lorenzo. In preservative the dorsum is dark brown with lighter mottling. There is little doubt that the specimen from San Lorenzo is a *Syrrhophus leprus*, an abundant and widespread species in the humid Gulf lowlands of southern México, and not *verruculatus*, if this is a valid species (see Firschein, *op. cit.*:58), and not *cystignathoides*, a species known from San Luis Potosí southward to central Veracruz.

Syrrhophus pipilans pipilans Taylor

Oaxaca: Cerro Arenal; Cerro San Pedro; 6 km. N of Chivela; 14 km. W of Tehuantepec (2).

In the isthmian region this frog is known only from the Pacific slopes and the Plains of Tehuantepec. Males call from the ground and from trees to heights of about four meters. The call is a single, high, long "peep."

Engystomops pustulosus Cope

Oaxaca: Chivela; La Ventosa (3); Santo Domingo; Tapanatepec (14); Tehuantepec (61); Unión Hidalgo (62). *Veracruz:* Acayucan; Cuatotolapam (7); 10 km. SE of Hueyapan (11).

Large congregations were breeding at Tehuantepec on July 5, at Tapanatepec on July 13, and at Hueyapan on July 24, 1956. The frogs were breeding in open ponds in scrub forest and savanna; none was found in the rainforest. Males call while floating on the water (Pl. 7, fig. 1); the call is a soft "do-ing, do-ing" with a rising tone on the last note. Numerous individual egg masses were along the bank of a pond near Tehuantepec; one large composite egg mass there had a surface area of about one square meter (Pl. 7, fig. 2). The large series from Unión Hidalgo was obtained by digging specimens out of a dry sandy river bank in the dry season. Some of the individuals were buried to a depth of 25 centimeters.

In life individuals from the Pacific lowlands were dull brown and gray; those from Acayucan were dark chocolate brown to black with pink or red blotches, forearms, and dorsal stripe. Not all specimens from the Atlantic lowlands are so colored; individuals

from Cordoba and Mirador, Veracruz, are like those from Tehuantepec.

Leptodactylus labialis Cope

Oaxaca: Agua Caliente; Chivela (2); Matías Romero (12); 33 km. N of Matías Romero (4); Mixtequilla; Santa Efigenia; Tapanatepec; Tehuantepec (38); Tolosita (2); 33 km. W of Zanatepec (49). *Veracruz:* Acayucan (3); Ciudad Alemán; Cuatotolapam (10); Hueyapan; La Oaxaqueña (4); 38 km. SE of Jesús Carranza; 20 km. ENE of Jesús Carranza; Novillero (3); San Lorenzo (2).

Although *Leptodactylus labialis* does not appear to be so abundant as *Leptodactylus melanonotus*, the former was found throughout the lowlands of the isthmus. In the dry season individuals were found along streams, and in the rainy season breeding congregations were found in rain pools, marshes, ponds, and even small puddles. The call is a slow "wort, wort, wort." Males call beneath the water and from beneath rocks and from holes in the ground. The average snout-vent length of eight adult males is 37.2 mm. A completely metamorphosed juvenile obtained at Hueyapan on July 24, 1956, has a snout-vent length of 11 mm.

Leptodactylus melanonotus Hallowell

Oaxaca: Agua Caliente (25); Cerro Arenal (2); Cerro Quiengola (3); Cerro San Pedro (3); Chivela (2); Coyol; Juchitán; Matías Romero (11); Mixtequilla (2); Papaloapan (2); Salazar (9); Salina Cruz; 11 km. S of Santiago Chivela; Tapanatepec (17); Tehuantepec (176); Tolosita; Unión Hidalgo; 27 km. W of Zanatepec (6). *Veracruz:* Acayucan; Cuatotolapam (9); Cosoleacaque; 20 km. ENE of Jesús Carranza (2); 20 km. SE of Minatitlán (2); Novillero; San Lorenzo (6).

This frog is abundant throughout the lowlands of the isthmus, where in the dry season individuals were found along streams and beneath rocks at a spring seepage. In the rainy season males were calling from nearly every bit of standing water. The call is a soft clicking sound resembling that made by striking two small stones together. The average snout-vent length of ten adult males is 41.8 mm. There is considerable variation in the extent of the yellowish brown glandular areas on the belly. Some have none, whereas others have a broad area on the chest, a band along the flanks, and a thin band across the lower abdomen. Individuals collected in the dry season vary in the same fashion as do those collected in the rainy season, at which time they were breeding. The glands are equally well-developed in adults of both sexes, and were present in some juveniles with snout-vent lengths of less than 20 mm. Apparently the development of the glands is not associated with maturity, sex, or size.

Diaglena reticulata Taylor

Oaxaca: Cerro Arenal; Chivela; Salina Cruz (26); San Antonio (3); Tehuantepec (2); 8.6 km. W of Tehuantepec (11); Zarzamora.

Breeding congregations of this rare frog were found 8.6 kilometers west of Tehuantepec on July 5, 1956, and at Salina Cruz on July 6, 1958. Both choruses took place immediately after torrential rains. In both instances the frogs were in and about open muddy pools in the scrub forest (Pl. 5, fig. 2); males called from the bank near the water, and clasping pairs were found only on land (Pl. 8, figs. 1-2). The call is a loud, nasal "braaa," two to three seconds in duration. Amplexus is axillary.

The dorsal ground color is light yellowish green tending towards olive on the head and fading to yellow on the flanks. The ventral surfaces, including the vocal sac, are white; the iris is golden and flecked with black. The present series agrees well with the description of *reticulata* (based on two specimens) given by Taylor (1942:60). A detailed analysis of variation, comparison with related species, and descriptions of tadpoles are reserved for a future report.

Hyla baudini Duméril and Bibron

Oaxaca: Bisilana; Cerro Quiengola (2); Cerro San Pedro; Coyol; Matías Romero (12); Mixtequilla; Río Sarabia (7); Salazar; San Antonio; 11 km. S of Santiago Chivela; Santo Domingo (3); Tapanatepec (2); Tehuantepec (23); Tolosita. *Veracruz:* Acayucan; Amatitlán; Ciudad Alemán (3); Cosamaloapan (2); Cuatotolapam (15); 10 km. SE of Hueyapan; 20 km. S of Jesús Carranza; 38 km. S of Jesús Carranza (2); 20 km. ENE of Jesús Carranza (4); La Oaxaqueña (2); Minatitlán (2); Naranja (3); Novillero (9); Río de las Playas (2); San Lorenzo (5); Tapalapan (2).

Commonly found on both sides of the isthmus, this large tree frog nearly always is associated with trees; it is not found in the savannas, although it breeds in savannas adjacent to rainforest. It appears to be somewhat more abundant in scrub forest than in rainforest. In the daytime individuals were found under the outer sheaths of banana plants, in the axills of leaves of elephant ears (*Xanthosoma*), in cavities in trees, and on shaded limbs in the forest. Recently metamorphosed individuals having snout-vent lengths slightly more than 20 mm. were found in the latter part of July.

Hyla ebraccata Cope

Oaxaca: Donají (17); 43 km. N of Matías Romero (27); Sarabia (6); Tolosita (3); Ubero (17). *Veracruz:* Aquilera.

This small species was found only in forested areas, where calling males were on bushes and trees around rain pools. The call

is a harsh squawk repeated at intervals of 15 to 20 seconds, followed by a minute or more of silence, and then repeated. Clasping pairs were found on bushes and in the water.

The dorsum bears a dark chocolate brown hour glass-shaped mark, which in some individuals is broken into a large mark posteriorly and a smaller triangular one on the head and nape. The dorsal ground color varies from pale cream or ivory to yellow or tan. The intensity of the dorsal pigmentation is subject to rather rapid change. The flanks, hands, and anterior part of the venter are lemon yellow; the feet, thighs, and posterior part of the venter are golden yellow. The dorsal surface of the shank is yellow to tan with chocolate brown bars or spots; the heel is pale yellow. There is a dark brown bar in the loreal region and a dark brown bar extending posteriorly from the eye to a point above the insertion of the forelimb. The iris is a copper color. The toes are completely webbed; the fingers, one-third webbed. There is a small axillary web that is evident when the forelimbs are at right angles to the body. Twenty males have an average snout-vent length of 28.1 mm.; three females, 35.3 mm. There are no nuptial tuberosities on the pollex of breeding males.

This species has been collected at Coyame and Catemaco in Los Tuxtlas and at various localities in Tabasco; it apparently ranges eastward from southern Veracruz, México, in humid forests to El Petén, Guatemala.

Hyla loquax Gaige and Stuart

Oaxaca: Donají (7); 43 km. N of Matías Romero (21). *Veracruz:* 19 km. N of Acayucan (4); Aquilera (3); 8 km. SW of Coatzacoalcos (36); Cuototolapam (11); Naranja (13); San Lorenzo (3).

In the isthmus this species is known only from the humid forests of the Gulf lowlands; it is also known from Boca del Río, Veracruz, and from Teapa and Villa Hermosa, Tabasco.

Calling males were found on aquatic plants above the water in deep ponds in the forest where it was necessary for the collector to wade waist-deep in water to obtain them. The call is a loud "hah-onk." Individuals, when active at night, are yellowish tan above with light olive green spots. The flanks, belly, and vocal sac are yellow, and the anterior and posterior surfaces of the thighs and webbing of the feet are bright orange-red or tomato red. Individuals found during the day are grayish brown with olive markings or reddish brown with black markings. Sleeping individuals are ivory-gray with faint gray markings. The iris is a bright copper color. Fifteen adult males have an average snout-vent length of

41.7 mm.; they have no horny nuptial pads on the pollex.

The relationships of this species are with *Hyla rickardsi* Taylor, a species known only from the foothills of the Sierra Madre Oriental in the states of Puebla and Veracruz. The distinguishing characteristics of these species are given in Table 1. Living individuals may be distinguished immediately by the flash colors on the thighs—red in *loquax* and yellow in *rickardsi.* The calls of the two species are distinctly different; that of *rickardsi* is a high-pitched, loud rattle continued for several seconds, notably different from the goose-like honk of *loquax.*

TABLE 1.—COMPARISON OF CERTAIN CHARACTERS IN HYLA LOQUAX AND HYLA RICKARDSI

CHARACTER	*loquax*	*rickardsi*
Toe webbing	Full	Three-fourths
Finger webbing	Three-fourths	One-half
Average snout-vent length (♂)	41.7 mm.	37.4 mm.
Tympanum/eye (♂)	63.2%	55.8%
Dorsal leg pattern	Barred	Unmarked
Tarsal fold	Tubercular	Absent
Tarsal stripe	Absent or indistinct	Broad, indistinct, or absent
Dorsolateral stripe	Absent	Present
Light line over anus	Broad	Narrow
Flash colors	Red	Yellow
Iris color	Copper	Bronze

The three specimens from San Lorenzo, Veracruz (USNM 123513-5), were identified as *Hyla rickardsi* by Smith (1947:409). The flash colors have faded in preservative, and so are of no aid in identifying these specimens. Two are adult females with snout-vent lengths of 35 and 39 mm. In possessing a relatively large tympanum and barred thighs, and in lacking a dorsolateral stripe they are typical of *loquax,* but in the amount of webbing on the hands and feet, broad tarsal stripe, and narrow anal stripe they are like *rickardsi.* The third specimen, a juvenile, has a snout-vent length of 25 mm. In coloration it resembles the adults; it has more distinct

bars on the limbs. On the basis of geography these specimens should be *loquax*, for the closest known record of *rickardsi* is more than 200 kilometers to the northwest, whereas *loquax* is known from several localities around San Lorenzo.

Shannon and Werler (1955:383) described *Hyla axillamembrana* from the lower southern slopes of Los Tuxtlas. The unique type is a small male (27 mm. snout-vent). I have examined the type and find no great differences between it and small specimens of *loquax*. It is not possible to determine the color of the thighs, nor was this information given in the description. *Hyla axillamembrana* is here considered to be a synonym of *Hyla loquax*.

Hyla microcephala martini Smith

Oaxaca: Donají (15); 43 km. N of Matías Romero (19); Río Sarabia (2); Sarabia (11); Tolosita. *Veracruz:* Acayucan (17); Alvarado (41); Aquilera (21); 8 km. SW of Coatzacoalcos (10); Cosoleacaque (26); 10 km. SE of Hueyapan; Naranja (3); Novillero.

This frog is abundant in the Gulf lowlands of the isthmus, where large breeding congregations were found in grassy ponds on the savannas and in openings in the forest. Most frequently males were calling from grasses and reeds in the ponds; many individuals were perched precariously on thin blades as high as one meter above the water. The call is a series of low squeaks.

Individuals found at night were pale yellow above with light brown lines arranged in an irregular pattern on the back, but often forming a cross or an X-shaped mark in the scapular region. There is a brown stripe from the nostril to the eye and thence to the groin. Anteriorly this stripe is bordered above by a thin white or cream-colored line. Numerous small brown flecks are scattered on the back and dorsal surface of the shank. In most specimens there are thin transverse brown bars on the shank. The thighs and undersides of the limbs are golden yellow; the belly and vocal sac are lemon yellow. The iris is yellowish brown. During the day individuals assume a pale reddish tan ground color with darker brown markings. Twenty-five adult males from Alvarado have an average snout-vent length of 24.1 mm.

Hyla picta Günther

Oaxaca: Donají (8); Sarabia (11); Tolosita (15); Ubero (6). *Veracruz:* 19 km. N of Acayucan (4); Alvarado (5); Aquilera; 8 km. SW of Coatzacoalcos; 10 km. SE of Hueyapan (7); Lerdo de Tejada; Tula (3).

Widespread in the forests, scrub, and savannas on the Gulf lowlands of the isthmus, these frogs were found breeding at numerous localities. Males call from grasses and bushes growing in and

about ponds. The call is a high-pitched insect-like trill. At night these frogs are pale yellow above; they change to light grayish tan during the day. A dark stripe extends from the nostril to the eye and thence posteriorly to a point between the axilla and groin. Above this dark stripe is a broader white stripe. Scattered on the dorsum are brown flecks or spots; the shanks are marked with poorly-defined cross-bars. The thighs are deep yellow below and paler above with scattered dark flecks. The belly is white, and the vocal sac is yellow. The iris is golden. Twenty males have an average snout-vent length of 21.5 mm.; three females, 24.0 mm.

Hyla robertmertensi Taylor

Oaxaca: Tapanatepec (28); 7.5 km. NW of Tapanatepec (38); 7.2 km. WNW of Zanatepec (77).

This species was found in the isthmian region only on the Pacific lowlands at the southern base of the western part of the Sierra Madre de Chiapas. On July 13, 1956, many large choruses were discovered. The calling males were on reeds and thorn scrub in and at the edge of temporary ponds; the call is a cricket-like "creak-creack," quickly followed by a series of notes "creak-eek-eek-eek-eek."

At night the dorsal ground color is pale yellow; this changes to pinkish buff during the day. There is a grayish or brown dark stripe from the nostril to the eye; the stripe continues to the groin. This dark stripe is bordered above by a narrow white stripe. The belly is white, and the vocal sac is yellow. The iris is dull reddish brown. Twenty-five males have an average snout-vent length of 24.7 mm.

Hyla staufferi Cope

Oaxaca: Chivela; Huilotepec (5); Juchitán (4); Matías Romero (4); 25 km. N of Matías Romero; Mixtequilla (4); Río Sarabia (11); 11 km. S of Santiago Chivela; Sarabia (3); Tapanatepec (67); Tehuantepec (66); Tolosita (2); Ubero; Unión Hidalgo; Zanatepec (6). *Veracruz:* Acayucan (7); Alvarado (3); Amatitlán; Aquilera; Ciudad Alemán (3); 8 km. SW of Coatzacoalcos (9); Cosamaloapan (4); Cosoleacaque (8); 10 km. SE of Hueyapan; Lerdo de Tejada; Novillero (6); Tula (2).

This is the only species of small hylid that crosses the isthmus. Calling males were found in and about ponds on the savannas in southern Veracruz, in ponds in open forest in northern Oaxaca (not in forest pools), and in temporary pools in the scrub forest on the Pacific lowlands. Individuals usually called from bushes and reeds in or at the edge of ponds. The call is a short "braaa." Dates of breeding choruses indicate that by the time the other small species of hylids in the Gulf lowlands reach the peak of their

breeding season, that of *H. staufferi* is essentially over; no large breeding congregations were found in July. On July 8, 1956, two metamorphosing young were found clinging to blades of grass in a pond; they had snout-vent lengths of 8 and 9 mm. and tail stumps less than 3 mm. in length. Others were found on July 13 and 26. The juveniles are nearly unicolor olive green above and white below.

In life the adults vary greatly in color pattern. The dorsal ground color is yellowish tan to olive brown with olive brown or dark brown spots, some of which in certain individuals are connected to form longitudinal dark stripes. On the posterior surface of the thighs are small white flecks. The belly is white, and the vocal sac is a rich yellow. Twenty males have an average snout-vent length of 26.3 mm.; they have no horny nuptial pads. No noticeable differences in either color or body proportions were found between the populations on either side of the isthmus.

Hylella sumichrasti Brocchi

Oaxaca: Cerro Arenal (5); Cerro San Pedro (2); Escurano; La Concepción (41); Portillo Los Nanches (6); San Antonio (16); 11 km. S of Santiago Chivela (18); Santa Lucía (7); Tapanatepec (5); Tehuantepec (8); Tenango (49); Tres Cruces (19).

With the exception of the series from 11 kilometers south of Santiago Chivela, most of these specimens were found in small arboreal bromeliads during the dry season. Males were found along a clear, shallow, rocky stream south of Santiago Chivela on July 6, 1956. The frogs were calling from bushes and rocks in and along the stream. When disturbed, they jumped into the water and floated downstream until they were able to hold onto a rock or other object. The call is a loud "bra-a-ah." In breeding individuals the dorsum is pale yellow; the belly is white, and the vocal sac is yellow. The iris is pale golden yellow. Eighteen males have an average snout-vent length of 25.2 mm. All have dark brown nuptial tuberosities on the pollex.

Certain diagnostic characters of this species as given by Taylor (1943a:50) and Taylor and Smith (1945:598) are in need of revision. *Hylella sumichrasti* has been characterized as having no vocal sac, rarely having vomerine teeth, and as having a relatively smooth throat. The vocal sac in breeding males is quite evident; it is single, median, and when expanded, spherical. The openings into the vocal sac are narrow slits along the inner posterior border of the jaw rami. Of 151 specimens studied, 74 have vomerine